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# Chapter 1

# Introduction

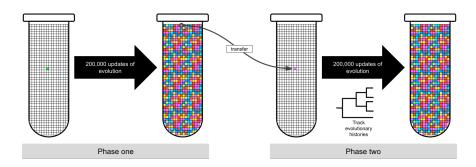


Figure 1.1: Experimental design overview

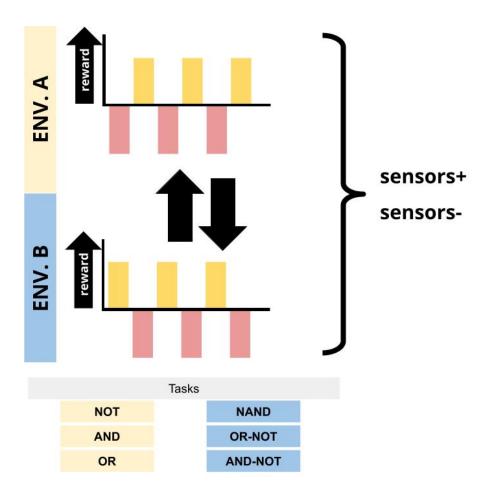


Figure 1.2: Fluctuating environment

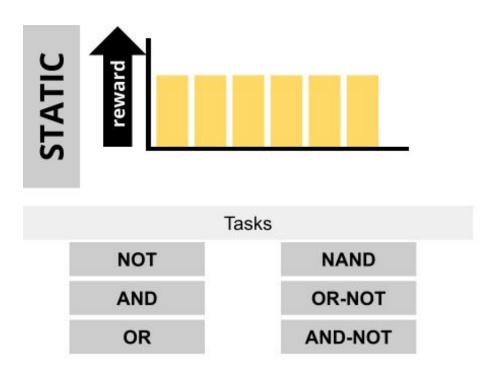


Figure 1.3: Static environment

### Chapter 2

### Validation experiment

In this experiment, we validate that (1) we observe the evolution of phenotypic plasticity in a changing environment when digital organisms have access to sensory instructions (capable of differentiating environmental states) and (2) that adaptive phenotypic plasticity does not evolve when populations lack access to sensory instructions.

#### 2.1 Overview

```
total_updates <- 200000
replicates <- 100

all_traits <- c("not", "nand", "ornot", "or", "andnot")
traits_set_a <- c("not", "and", "or")
traits_set_b <- c("nand", "ornot", "andnot")

# Relative location of data.
working_directory <- "experiments/2021-01-07-validation/analysis/"
# working directory <- "./"
# << For bookdown
# << For local analysis</pre>
```

We evolved populations of digital organisms under four conditions:

- 1. A fluctuating environment with access to sensory instructions
- 2. A fluctuating environment without access to sensory instructions (i.e., sensory instructions are no-operations)
- 3. A constant environment with access to sensory instructions
- 4. A constant environment without access to sensory instructions

In fluctuating environments, we alternate between rewarding and punishing different sets of computational tasks. In one environment, we reward tasks not,

and, or and punish tasks nand, ornot, andnot. In the alternative environment, we reward tasks nand, ornot, andnot and punish tasks not, and, or. In constant environments, we reward all tasks (not, nand, and, ornot, or, andnot).

For each replicate of each condition, we extract the dominant (i.e., most numerous) genotype at the end of the run to analyze further. We expect to observe the evolution of adaptive phenotypic plasticity in only the first experimental condition. In conditions without sensors, plasticity in any form should be unable to evolve.

#### 2.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd9
```

These analyses were conducted/knitted with the following computing environment:

```
print(version)
```

```
x86 64-pc-linux-gnu
## platform
## arch
                  x86_64
## os
                  linux-gnu
## system
                  x86_64, linux-gnu
## status
                  4
## major
## minor
                  0.4
                  2021
## year
## month
                  02
                  15
## day
                  80002
## svn rev
## language
## version.string R version 4.0.4 (2021-02-15)
## nickname
                  Lost Library Book
```

### 2.3 Setup

```
data_loc <- paste0(working_directory, "data/aggregate.csv")
data <- read.csv(data_loc, na.strings="NONE")
data$DISABLE_REACTION_SENSORS <- as.factor(data$DISABLE_REACTION_SENSORS)</pre>
```

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```
data$chg_env <- as.factor(data$chg_env)</pre>
data$dom_plastic_odd_even <- as.factor(data$dom_plastic_odd_even)</pre>
data$sensors <- data$DISABLE_REACTION_SENSORS == "0"</pre>
data$is_plastic <- data$dom_plastic_odd_even == "True"</pre>
env_label_fun <- function(chg_env) {</pre>
 if (chg_env) {
    return("Fluctuating")
  } else {
    return("Constant")
 }
}
sensors_label_fun <- function(has_sensors) {</pre>
  if (has_sensors) {
   return("Sensors")
 } else {
    return("No sensors")
 }
}
# Count observed plasticity for each condition (I'm sure there's a 'tidier' way to do this..)
observed_plasticity <- data.frame(</pre>
  environment=character(),
  sensors=character(),
  plastic=integer(),
  nonplastic=integer(),
  plastic_adaptive=integer(),
  plastic optimal=integer(),
  plastic_nonadaptive=integer()
for (env_chg in levels(data$chg_env)) {
  for (disabled_sensors in levels(data$DISABLE_REACTION_SENSORS)) {
    cond_data <- filter(data, chg_env == env_chg & data$DISABLE_REACTION_SENSORS == disabled_sens
    environment_label <- env_label_fun(env_chg)</pre>
    sensors_label <- sensors_label_fun(disabled_sensors == "0")</pre>
    observed_plasticity <- observed_plasticity %>% add_row(
      environment=environment_label,
      sensors=sensors_label,
      plastic=nrow(filter(cond_data, is_plastic==TRUE)),
      nonplastic=nrow(filter(cond_data, is_plastic==FALSE)),
      plastic_adaptive=nrow(filter(cond_data, dom_adaptive_plasticity=="True")),
      plastic_optimal=nrow(filter(cond_data, dom_optimal_plastic=="True")),
      plastic_nonadaptive=nrow(filter(cond_data, is_plastic==TRUE & dom_adaptive_plasticity=="Fal
```

```
}

observed_plasticity <- pivot_longer(
  observed_plasticity,
  cols=c("plastic", "plastic_adaptive", "plastic_optimal", "plastic_nonadaptive", "nongonames_to="phenotype",
  values_to="phenotype_cnt"
)

####### misc ######

# Configure our default graphing theme
theme_set(theme_cowplot())
</pre>
```

### 2.4 Evolution of phenotypic plasticity

For each experimental condition, do we observe the evolution of phenotypic plasticity? To test for phenotypic plasticity, we culture digital organisms in both environments from the fluctuating condition (including organisms evolved in a constant environment). Any plasticity that we observe from digital organisms evolved under constant conditions is cryptic variation (as these organisms were never exposed to these culturing environments).

```
ggplot(filter(observed_plasticity, phenotype %in% c("plastic", "nonplastic")), aes(x=p)
  geom_bar(
    stat="identity",
    position=position_dodge(0.9)
  geom_text(
    stat="identity",
   mapping=aes(label=phenotype_cnt),
   vjust=0.05
  ) +
 scale_fill_brewer(palette="Accent") +
  scale_x_discrete(
   name="Phenotype",
   limits=c("plastic", "nonplastic"),
   labels=c("Plastic", "Non-plastic")
  ) +
 facet_grid(sensors~environment) +
 theme(
    legend.position="none"
```



Indeed, we do not observe the evolution of phenotypic plasticity in any replicates in which digital organisms do not have access to sensory instructions. We do observe the evolution of plasticity (not necessarily adaptive plasticity) in both constant and fluctuating environments where sensors are enabled.

To what extent is the observed phenotypic plasticity adaptive?

```
ggplot(filter(observed_plasticity, environment=="Fluctuating" & sensors == "Sensors" & phenotype
  geom_bar(
   stat="identity",
   position=position_dodge(0.9)
  geom_text(
    stat="identity",
   mapping=aes(label=phenotype_cnt),
   vjust=0.05
  ) +
  scale_fill_brewer(palette="Accent") +
  scale_x_discrete(
   name="Phenotype",
   limits=c("plastic", "plastic_adaptive", "plastic_optimal", "plastic_nonadaptive"),
   labels=c("Total plastic", "Adaptive plasticity", "Optimal plasticity", "Non-adaptive plastic
  ) +
  facet_grid(sensors~environment) +
  theme(
    legend.position="none"
```



### Chapter 3

### Evolutionary change

The effect of adaptive phenotypic plasticity on evolutionary change.

#### 3.1 Overview

```
total_updates <- 200000
replicates <- 100

all_traits <- c("not", "nand", "ornot", "or", "andnot")
traits_set_a <- c("not", "and", "or")
traits_set_b <- c("nand", "ornot", "andnot")

# Relative location of data.
working_directory <- "experiments/2021-02-08-evo-dynamics/analysis/" # << For bookdown
# working_directory <- "./"
# << For local analysis</pre>
```

### 3.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
library(RColorBrewer)
library(Hmisc)
library(boot)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd97121f7f9ce9
```

These analyses were conducted/knitted with the following computing environ-

```
ment:
```

```
print(version)
##
                  x86_64-pc-linux-gnu
## platform
## arch
                  x86_64
## os
                  linux-gnu
                  x86_64, linux-gnu
## system
## status
## major
## minor
                  0.4
                  2021
## year
## month
                  02
## day
                  15
## svn rev
                  80002
## language
                  R
## version.string R version 4.0.4 (2021-02-15)
## nickname
                  Lost Library Book
```

### 3.3 Setup

```
summary_data_loc <- paste0(working_directory, "data/aggregate.csv")</pre>
summary_data <- read.csv(summary_data_loc, na.strings="NONE")</pre>
summary_data$DISABLE_REACTION_SENSORS <- as.factor(summary_data$DISABLE_REACTION_SENSO
summary_data$chg_env <- summary_data$chg_env == "True"</pre>
summary_data$dominant_plastic_odd_even <- as.factor(summary_data$dominant_plastic_odd_.
summary_data$sensors <- summary_data$DISABLE_REACTION_SENSORS == "0"</pre>
summary_data$is_plastic <- summary_data$dominant_plastic_odd_even == "True"
env_label_fun <- function(chg_env) {</pre>
  if (chg_env) {
   return("Fluctuating")
 } else {
    return("Constant")
 }
sensors_label_fun <- function(has_sensors) {</pre>
  if (has sensors) {
   return("Sensors")
 } else {
    return("No sensors")
```

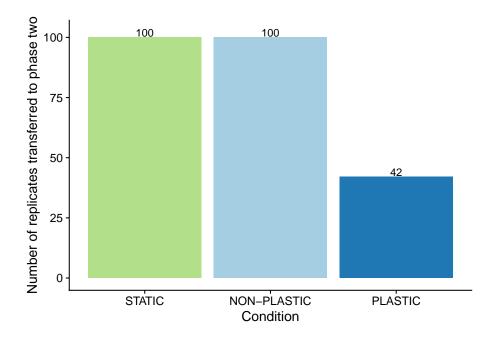
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```
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
 } else if (env_chg) {
    return("NON-PLASTIC")
 } else {
    return("STATIC")
 }
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
)
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
)
summary_data$condition <- mapply(</pre>
  condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
condition_order = c(
 "STATIC",
 "NON-PLASTIC",
 "PLASTIC"
)
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
# Create a directory to store plots
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
# Define sample mean function
samplemean <- function(x, d) {</pre>
  return(mean(x[d]))
}
```

### 3.4 The evolution of phenotypic plasticity

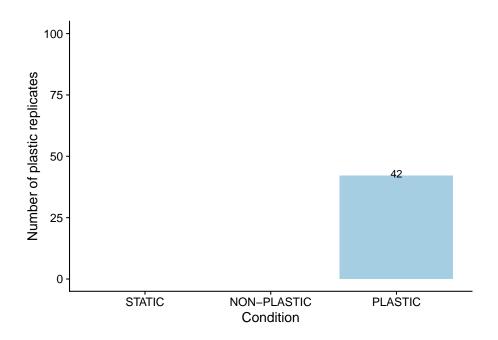
For sensor-enabled populations in fluctuating environments, we only transferred populations containing an optimally plastic genotype to phase-two.

```
summary_data_grouped = dplyr::group_by(summary_data, condition)
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
  geom_col(position=position_dodge(0.9)) +
 geom_text(aes(label=n, y=n+2)) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  scale fill brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
 ylab("Number of replicates transferred to phase two") +
 theme(
   legend.position="none"
```

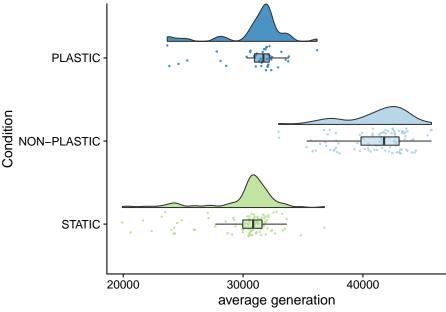


We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

```
summary_data_grouped = dplyr::group_by(summary_data, condition, is_plastic)
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
  geom_col(
   position=position_dodge(0.9)
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  geom_text(aes(label=n, y=n+1)) +
  ylab("Number of plastic replicates") +
  ylim(0, 100) +
  theme(
    legend.position="none"
```



```
ggprot(Summary_data, aes(x-condition, y-time_average_generation, fifth-condition)) +
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 scale_fill_brewer(
   palette="Paired"
 ) +
 scale_color_brewer(
  palette="Paired"
 ) +
 coord_flip() +
 ylab("average generation") +
 theme(
   legend.position="none"
 ggsave(paste0(working_directory, "plots/", "average-generation.png"))
```



```
paste0(
  "PLASTIC median: ",
  median(filter(summary_data, condition=="PLASTIC")$time_average_generation)
## [1] "PLASTIC median: 31697.65"
paste0(
  "STATIC median: ",
  median(filter(summary_data, condition=="STATIC")$time_average_generation)
## [1] "STATIC median: 30839.75"
paste0(
  "NON-PLASTIC median: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$time_average_generation)
## [1] "NON-PLASTIC median: 41768.65"
kruskal.test(
  formula=time_average_generation~condition,
  data=summary_data
)
##
## Kruskal-Wallis rank sum test
```

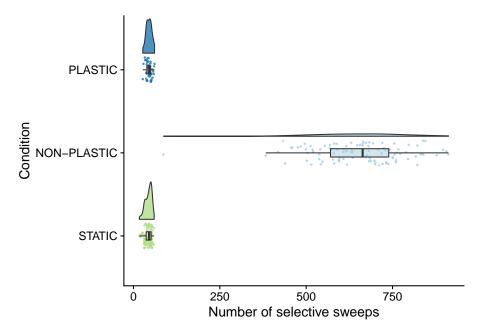
```
##
## data: time_average_generation by condition
## Kruskal-Wallis chi-squared = 177.33, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$time_average_generation,
  g=summary_data$condition,
 p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: summary_data$time_average_generation and summary_data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.004
## P value adjustment method: bonferroni
```

#### 3.6 Selective sweeps

The number of times the most recent common ancestor changes gives us the number of selective sweeps that occur during the experiment.

```
ggplot(summary_data, aes(x=condition, y=phylo_mrca_changes, fill=condition)) +
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale fill brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
```

```
palette="Paired"
) +
coord_flip() +
scale_x_discrete(
  name="Condition",
  limits=condition_order
) +
ylab("Number of selective sweeps") +
theme(
  legend.position="none"
)
```



```
paste0(
   "PLASTIC: ",
   median(filter(summary_data, condition=="PLASTIC")$phylo_mrca_changes)
)

## [1] "PLASTIC: 45.5"

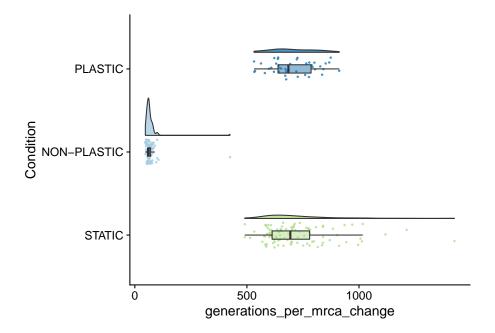
paste0(
   "STATIC: ",
   median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)
)

## [1] "STATIC: 45"
```

```
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$phylo_mrca_changes)
)
## [1] "NON-PLASTIC: 663.5"
kruskal.test(
  formula=phylo_mrca_changes~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
## data: phylo_mrca_changes by condition
## Kruskal-Wallis chi-squared = 175.46, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$phylo_mrca_changes,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: summary_data$phylo_mrca_changes and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
##
## P value adjustment method: bonferroni
```

# 3.6.1 Average number of generations between selective sweeps

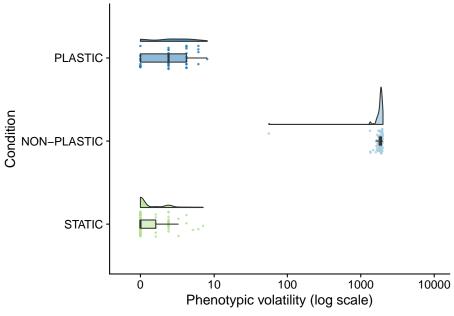
```
position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
  width = .1,
  outlier.shape = NA,
  alpha = 0.5
scale_x_discrete(
  name="Condition",
  limits=condition_order
) +
scale_fill_brewer(
  palette="Paired"
scale_color_brewer(
  palette="Paired"
coord_flip() +
theme(
  legend.position="none"
```



```
paste0(
  "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$generations_per_mrca_change)
)
## [1] "PLASTIC: 685.001780758557"
paste0(
 "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$generations_per_mrca_change)
## [1] "STATIC: 693.676265008576"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$generations_per_mrca_change)
## [1] "NON-PLASTIC: 62.0184902295191"
kruskal.test(
  formula=generations_per_mrca_change~condition,
  data=summary_data
##
## Kruskal-Wallis rank sum test
##
## data: generations_per_mrca_change by condition
## Kruskal-Wallis chi-squared = 175.33, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$generations_per_mrca_change,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: summary_data$generations_per_mrca_change and summary_data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       1
## P value adjustment method: bonferroni
```

# 3.7 Phenotypic volatility along the dominant lineage

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_volatility, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_y_continuous(
   name="Phenotypic volatility (log scale)",
   trans="pseudo_log",
   breaks=c(0, 10, 100, 1000, 10000),
   limits=c(-1,10000)
  ) +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
  theme(
   legend.position="none"
```



```
paste0(
  "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility)
## [1] "PLASTIC: 2"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility)
## [1] "STATIC: O"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volatil
## [1] "NON-PLASTIC: 1868"
kruskal.test(
  formula=dominant_lineage_trait_volatility~condition,
  data=summary_data
)
##
## Kruskal-Wallis rank sum test
```

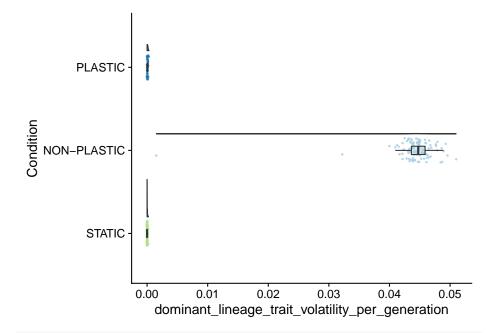
```
##
## data: dominant_lineage_trait_volatility by condition
## Kruskal-Wallis chi-squared = 190.78, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$dominant_lineage_trait_volatility,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary data$dominant lineage trait volatility and summary data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
## STATIC < 2e-16
                       8.7e-07
## P value adjustment method: bonferroni
```

## 3.7.1 Phenotypic volatility normalized by generations elapsed

```
summary_data$dominant_lineage_trait_volatility_per_generation <- summary_data_dominant_lineage_trait_volatility_per_generation <- summary_data_dominant_lineage_t
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_volatility_per_generation, fill=co
          geom_flat_violin(
                   position = position_nudge(x = .2, y = 0),
                   alpha = .8
          ) +
          geom_point(
                   mapping=aes(color=condition),
                   position = position_jitter(width = .15),
                   size = .5,
                   alpha = 0.8
          ) +
          geom_boxplot(
                   width = .1,
                   outlier.shape = NA,
                   alpha = 0.5
          ) +
          scale_x_discrete(
                   name="Condition",
                   limits=condition_order
```

## [1] "STATIC: 0"

```
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
)
```



```
paste0(
   "PLASTIC: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility_;
)

## [1] "PLASTIC: 6.33339279717772e-05"

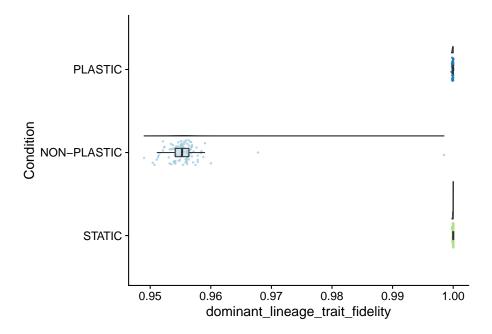
paste0(
   "STATIC: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility_p;
)
```

) +

geom\_point(

```
paste0(
  "NON-PLASTIC: ",
 median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volatility_per_ger
## [1] "NON-PLASTIC: 0.0447440145638177"
kruskal.test(
  formula=dominant_lineage_trait_volatility_per_generation~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
## data: dominant_lineage_trait_volatility_per_generation by condition
## Kruskal-Wallis chi-squared = 189.62, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$dominant_lineage_trait_volatility_per_generation,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: summary_data$dominant_lineage_trait_volatility_per_generation and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
## STATIC < 2e-16
                       4.2e-06
##
## P value adjustment method: bonferroni
3.7.2
       Phenotypic fidelity
Frequency that an offspring's genotype is identical to a parent genotype (along
the dominant lineage).
summary_data$dominant_lineage_trait_fidelity <- (summary_data$dominant_generation_born - summary_</pre>
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_fidelity, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
```

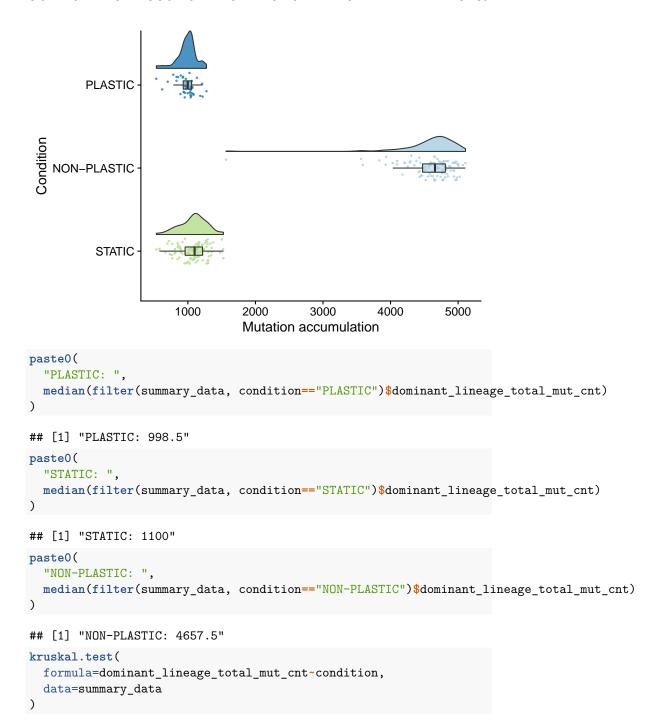
```
mapping=aes(color=condition),
  position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
geom_boxplot(
 width = .1,
  outlier.shape = NA,
  alpha = 0.5
) +
scale_x_discrete(
 name="Condition",
 limits=condition_order
scale_fill_brewer(
 palette="Paired"
) +
scale_color_brewer(
 palette="Paired"
coord_flip() +
theme(
  legend.position="none"
```



```
paste0(
 "PLASTIC: ",
 median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_fidelity)
## [1] "PLASTIC: 0.999936666072028"
paste0(
 "STATIC: ",
 median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_fidelity)
## [1] "STATIC: 1"
paste0(
 "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_fidelity)
## [1] "NON-PLASTIC: 0.955255985436182"
kruskal.test(
 formula=dominant_lineage_trait_fidelity~condition,
 data=summary_data
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_trait_fidelity by condition
## Kruskal-Wallis chi-squared = 189.62, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=summary_data$dominant_lineage_trait_fidelity,
 g=summary_data$condition,
 p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: summary_data$dominant_lineage_trait_fidelity and summary_data$condition
##
##
          NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
## STATIC < 2e-16
                       4.2e-06
## P value adjustment method: bonferroni
```

# 3.8 Mutation accumulation along the dominant lineage

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_total_mut_cnt, fill=condition
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ylab("Mutation accumulation") +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ) +
 scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
 coord_flip() +
 theme(
   legend.position="none"
```



## Kruskal-Wallis rank sum test

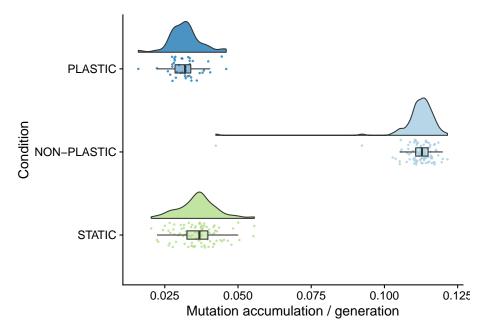
##

```
##
## data: dominant_lineage_total_mut_cnt by condition
## Kruskal-Wallis chi-squared = 179.33, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=summary_data$dominant_lineage_total_mut_cnt,
  g=summary_data$condition,
 p.adjust.method="bonferroni",
)
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary data$dominant lineage total mut cnt and summary data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.0019
## P value adjustment method: bonferroni
```

## 3.8.1 Mutation accumulation normalized by generations elapsed

```
summary data$mutations per generation <- summary data$dominant lineage total mut cnt /
ggplot(summary_data, aes(x=condition, y=mutations_per_generation, fill=condition)) +
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
    position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
    outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
    limits=condition_order
```

```
ylab("Mutation accumulation / generation") +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
)
```



```
paste0(
   "PLASTIC: ",
   median(filter(summary_data, condition=="PLASTIC")$mutations_per_generation)
)

## [1] "PLASTIC: 0.0319267181456982"

paste0(
   "STATIC: ",
   median(filter(summary_data, condition=="STATIC")$mutations_per_generation)
)
```

## [1] "STATIC: 0.0368157192941933"

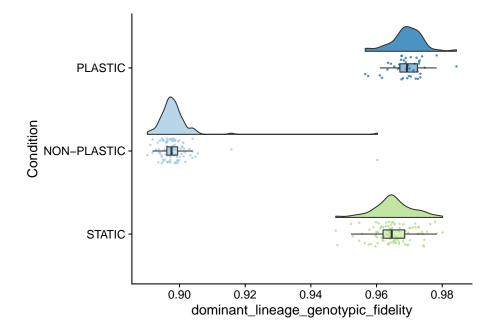
```
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$mutations_per_generation)
)
## [1] "NON-PLASTIC: 0.112804526786948"
kruskal.test(
  formula=mutations_per_generation~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
## data: mutations_per_generation by condition
## Kruskal-Wallis chi-squared = 180.11, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$mutations_per_generation,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: summary_data$mutations_per_generation and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       2e-04
##
## P value adjustment method: bonferroni
```

#### 3.8.2 Genotypic fidelity

The frequency that an offspring's genotype is the same as a parent's genotype.

```
summary_data$dominant_lineage_genotypic_fidelity <- (summary_data$dominant_generation_
ggplot(summary_data, aes(x=condition, y=dominant_lineage_genotypic_fidelity, fill=cond
    geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
    geom_point(
    mapping=aes(color=condition),</pre>
```

```
position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
  width = .1,
  outlier.shape = NA,
  alpha = 0.5
scale_x_discrete(
  name="Condition",
  limits=condition_order
) +
scale_fill_brewer(
  palette="Paired"
scale_color_brewer(
  palette="Paired"
) +
coord_flip() +
theme(
  legend.position="none"
```



```
paste0(
 "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_genotypic_fidelit
)
## [1] "PLASTIC: 0.969286906891951"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_genotypic_fidelity
## [1] "STATIC: 0.964620594632577"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_genotypic_fide
## [1] "NON-PLASTIC: 0.89754902563783"
kruskal.test(
  formula=dominant_lineage_genotypic_fidelity~condition,
  data=summary_data
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_genotypic_fidelity by condition
## Kruskal-Wallis chi-squared = 179.86, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$dominant_lineage_genotypic_fidelity,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: summary_data$dominant_lineage_genotypic_fidelity and summary_data$condition
##
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       2e-04
## P value adjustment method: bonferroni
```

# 3.9 Characterizing variation along dominant lineages

```
summary_data$frac_phenotype_changing_mut_steps <- summary_data$dominant_lineage_num_mut_steps_that
ggplot(summary_data, aes(x=condition, y=frac_phenotype_changing_mut_steps, fill=condition)) +
  geom flat violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition order
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
  theme(
   legend.position="none"
  ggsave(paste0(working_directory, "plots/", "frac_phenotype_changing_mutational_steps.png"))
```

```
PLASTIC - NON-PLASTIC - O.0 O.1 O.2 O.3 O.4 O.5 frac_phenotype_changing_mut_steps
```

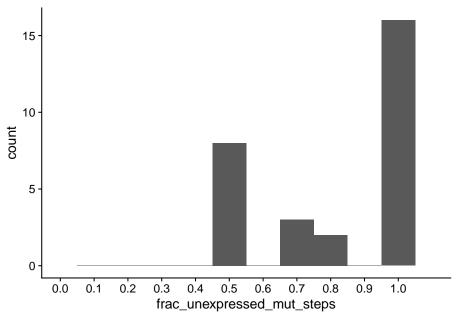
```
paste0(
  "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$frac_phenotype_changing_mut_steps)
## [1] "PLASTIC: 0.00224941742616098"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$frac_phenotype_changing_mut_steps)
## [1] "STATIC: O"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$frac_phenotype_changing_mut_st
## [1] "NON-PLASTIC: 0.437583018324547"
kruskal.test(
  formula=frac_phenotype_changing_mut_steps~condition,
  data=summary_data
##
## Kruskal-Wallis rank sum test
```

```
##
## data: frac_phenotype_changing_mut_steps by condition
## Kruskal-Wallis chi-squared = 191.23, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$frac_phenotype_changing_mut_steps,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$frac_phenotype_changing_mut_steps and summary_data$condition
##
           NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       2.3e-07
##
## P value adjustment method: bonferroni
```

## 3.9.2 For PLASTIC populations, what fraction of phenotype-altering mutations occurred in the

```
summary_data$frac_unexpressed_mut_steps <- summary_data$dominant_lineage_num_mut_steps_that_change
summary_data$frac_expressed_mut_steps <- summary_data$dominant_lineage_num_mut_steps_that_change_
ggplot(filter(summary_data, condition=="PLASTIC" & dominant_lineage_num_mut_steps_that_change_agg
geom_histogram(binwidth=0.1) +
scale_x_continuous(
   limits=c(0, 1.1),
   breaks=seq(0, 1.0, 0.1)
) +
theme(
legend.position="none"</pre>
```

## Warning: Removed 2 rows containing missing values (geom\_bar).



```
print(paste0("PLASTIC - Mean with bootstrapped 95% CI"))
## [1] "PLASTIC - Mean with bootstrapped 95% CI"
bo <- boot(filter(summary_data, condition=="PLASTIC" & dominant_lineage_num_mut_steps_
print(bo)
##
## ORDINARY NONPARAMETRIC BOOTSTRAP
##
##
## Call:
## boot(data = filter(summary_data, condition == "PLASTIC" & dominant_lineage_num_mut_:
       0) $frac_unexpressed_mut_steps, statistic = samplemean, R = 10000)
##
##
##
## Bootstrap Statistics :
        original
                       bias
                               std. error
## t1* 0.8247126 0.0002833333 0.03961207
print(boot.ci(bo, conf=0.95, type="perc"))
## BOOTSTRAP CONFIDENCE INTERVAL CALCULATIONS
## Based on 10000 bootstrap replicates
##
## CALL :
## boot.ci(boot.out = bo, conf = 0.95, type = "perc")
```

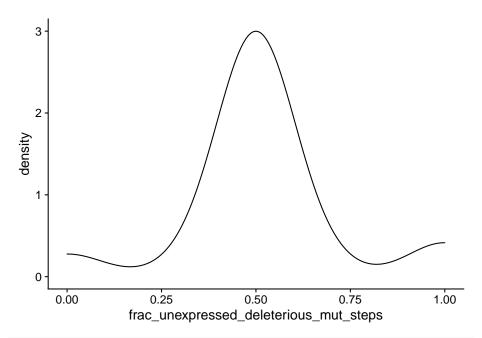
#### 3.9. CHARACTERIZING VARIATION ALONG DOMINANT LINEAGES45

# 3.9.3 For PLASTIC populations, what fraction of mutations that affect the unexpressed phenotype are deleterious versus beneficial?

aggregate\_frac\_unexpressed\_deleterious\_mut\_steps <- sum(plastic\_summary\_data\$dominant\_lineage\_numaggregate\_frac\_unexpressed\_beneficial\_mut\_steps <- sum(plastic\_summary\_data\$dominant\_lineage\_num\_

#### 3.9.3.1 Deleterious mutations

```
summary_data$frac_unexpressed_deleterious_mut_steps <- summary_data$dominant_lineage_num_mut_step
ggplot(
   filter(summary_data, condition=="PLASTIC" & dominant_lineage_num_mut_steps_that_change_unexpress
   aes(x=frac_unexpressed_deleterious_mut_steps)
) +
   geom_density() +
   theme(
    legend.position="none"
)</pre>
```



bo <- boot(filter(summary\_data, condition=="PLASTIC" & dominant\_lineage\_num\_mut\_steps\_
print(bo)</pre>

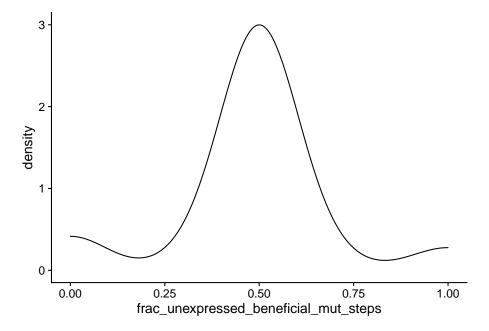
```
##
## ORDINARY NONPARAMETRIC BOOTSTRAP
##
##
## Call:
## boot(data = filter(summary_data, condition == "PLASTIC" & dominant_lineage_num_mut_
##
       0)$frac_unexpressed_deleterious_mut_steps, statistic = samplemean,
       R = 10000)
##
##
##
## Bootstrap Statistics :
        original
                        bias
                                std. error
## t1* 0.5172414 -0.0007335632 0.03944586
print(boot.ci(bo, conf=0.95, type="perc"))
## BOOTSTRAP CONFIDENCE INTERVAL CALCULATIONS
## Based on 10000 bootstrap replicates
## boot.ci(boot.out = bo, conf = 0.95, type = "perc")
## Intervals :
```

#### 3.9. CHARACTERIZING VARIATION ALONG DOMINANT LINEAGES47

```
## Level Percentile
## 95% ( 0.4402,  0.5943 )
## Calculations and Intervals on Original Scale
```

#### 3.9.3.2 Beneficial mutations

```
ggplot(
   filter(summary_data, condition=="PLASTIC" & dominant_lineage_num_mut_steps
   aes(x=frac_unexpressed_beneficial_mut_steps)
) +
   geom_density() +
   theme(
    legend.position="none"
```



bo <- boot(filter(summary\_data, condition=="PLASTIC" & dominant\_lineage\_num\_mut\_steps\_that\_change
print(bo)</pre>

```
##
## ORDINARY NONPARAMETRIC BOOTSTRAP
##
##
##
##
Call:
```

```
## boot(data = filter(summary_data, condition == "PLASTIC" & dominant_lineage_num_mut_:
       0)$frac_unexpressed_beneficial_mut_steps, statistic = samplemean,
       R = 10000)
##
##
##
## Bootstrap Statistics :
        original
                      bias
                               std. error
## t1* 0.4827586 0.0006393103 0.0390904
print(boot.ci(bo, conf=0.95, type="perc"))
## BOOTSTRAP CONFIDENCE INTERVAL CALCULATIONS
## Based on 10000 bootstrap replicates
##
## CALL :
## boot.ci(boot.out = bo, conf = 0.95, type = "perc")
##
## Intervals :
## Level
            Percentile
       (0.4057, 0.5586)
## 95%
## Calculations and Intervals on Original Scale
```

#### 3.10 Manuscript figures

Figures styled for the paper.

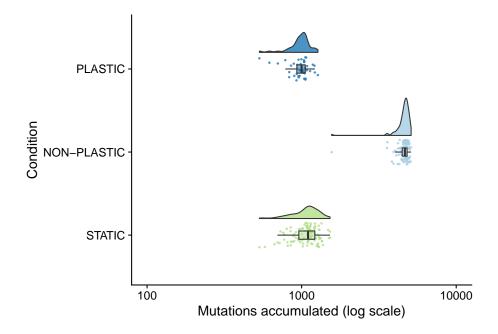
#### 3.10.1 Total evolutionary change

Selective sweeps, mutation accumulation, phenotypic volatility.

#### 3.10.1.1 Total mutation accumulation

```
mutation_count_fig <- ggplot(
    summary_data,
    aes(x=condition, y=dominant_lineage_total_mut_cnt, fill=condition)
) +
geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
) +</pre>
```

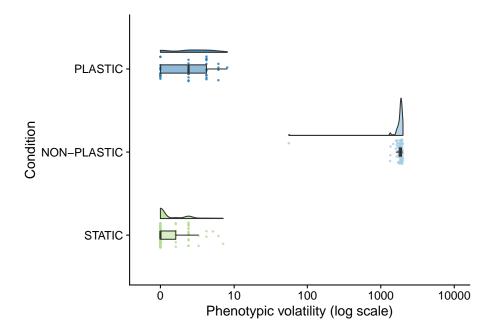
```
geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 ) +
 scale_y_continuous(
  name="Mutations accumulated (log scale)",
   trans="log10",
   breaks=c(100, 1000, 10000),
   limits=c(100, 10000)
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
 theme(
   legend.position="none"
  ggsave(
   pasteO(working_directory, "plots/", "mutation-accumulation.pdf"),
   width=5,
   height=4
 )
mutation_count_fig
```



#### 3.10.1.2 Phenotypic volatility

```
phenotypic_volatility_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_trait_volatility, fill=condition)
  ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  scale_x_discrete(
    name="Condition",
    limits=condition_order,
```

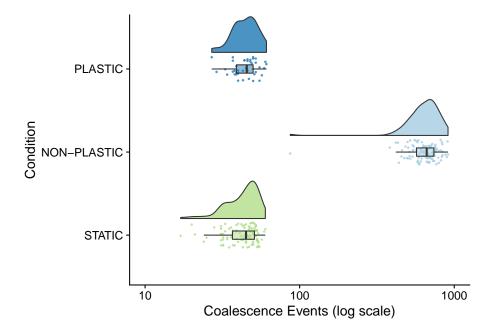
```
labels=condition_order
 ) +
 scale_y_continuous(
  name="Phenotypic volatility (log scale)",
  trans="pseudo_log",
  breaks=c(0, 10, 100, 1000, 10000),
   limits=c(-1,10000)
 ) +
 scale_fill_brewer(
   palette="Paired"
 scale_color_brewer(
   palette="Paired"
 ) +
 coord_flip() +
 theme(
   legend.position="none"
 ) +
 ggsave(
   pasteO(working_directory, "plots/", "phenotypic-volatility.pdf"),
   width=4,
   height=4
phenotypic_volatility_fig
```



#### 3.10.1.3 Coalescence events

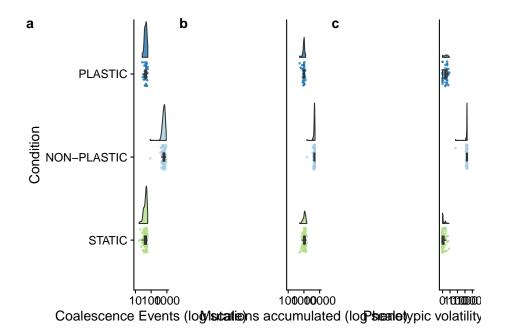
```
selective_sweeps_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=phylo_mrca_changes, fill=condition)
 ) +
 geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  scale_x_discrete(
    name="Condition",
    limits=condition_order,
```

```
labels=condition_order
 ) +
 scale_y_continuous(
  name="Coalescence Events (log scale)",
  trans="log10",
  breaks=c(10, 100, 1000),
   limits=c(10, 1000)
 ) +
 scale_fill_brewer(
   palette="Paired"
 scale_color_brewer(
   palette="Paired"
 ) +
 coord_flip() +
 theme(
   legend.position="none"
 ) +
 ggsave(
   pasteO(working_directory, "plots/", "selective-sweeps.pdf"),
   width=4,
   height=4
selective_sweeps_fig
```



#### **3.10.1.4** Combined

```
grid <- plot_grid(</pre>
  selective_sweeps_fig + theme(
    legend.position="none"
 ),
 mutation_count_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
    axis.title.y=element_blank()
 ),
 phenotypic_volatility_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
    axis.title.y=element_blank()
  ),
 nrow=1,
 align="v",
 labels="auto"
grid
```



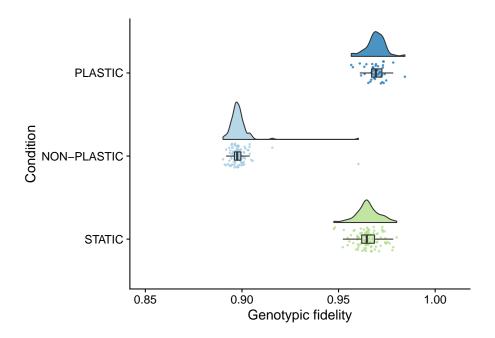
```
save_plot(
   paste0(working_directory, "plots/", "evolutionary-dynamics.pdf"),
   grid,
   base_height=6,
   base_asp=2.5
)
save_plot(
   paste0(working_directory, "plots/", "evolutionary-dynamics.png"),
   grid,
   base_height=6,
   base_asp=2.5
)
```

#### 3.10.2 Rate of evolutionary change

#### 3.10.2.1 Genotypic fidelity

```
genotypic_fidelity_fig <- ggplot(
    summary_data,
    aes(x=condition, y=dominant_lineage_genotypic_fidelity, fill=condition)
) +
geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +</pre>
```

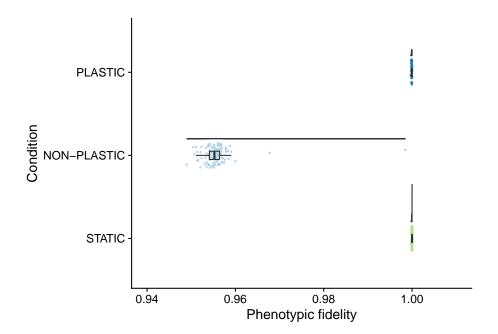
```
geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
    size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 ) +
 scale_y_continuous(
   name="Genotypic fidelity",
   limits=c(0.85, 1.01),
   breaks=c(0.85, 0.90, 0.95, 1.0) #seq(0.85, 1.0, 0.02)
 ) +
  scale_fill_brewer(
   palette="Paired"
 scale_color_brewer(
   palette="Paired"
 ) +
 coord_flip() +
 theme(
   legend.position="none"
 ) +
 ggsave(
   pasteO(working_directory, "plots/", "genotypic-fidelity.png"),
   width=5,
   height=4
  )
genotypic_fidelity_fig
```



#### 3.10.2.2 Phenotypic fidelity

```
phenotypic_fidelity_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_trait_fidelity, fill=condition)
 ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
    name="Condition",
    limits=condition_order,
```

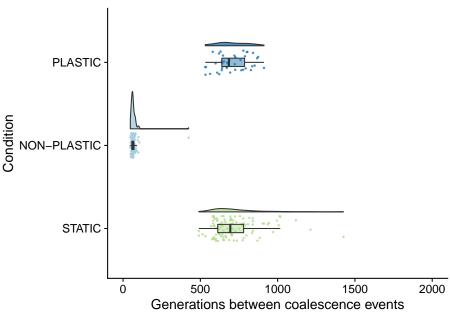
```
labels=condition_order
  scale_y_continuous(
   name="Phenotypic fidelity",
   limits=c(0.94, 1.01),
   breaks=c(0.94, 0.96, 0.98, 1.0) #seq(0.94, 1.0, 0.01)
  ) +
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  coord_flip() +
  theme(
    legend.position="none"
  ) +
  ggsave(
    pasteO(working_directory, "plots/", "phenotypic-fidelity.png"),
    width=4,
    height=4
  )
phenotypic_fidelity_fig
```



#### 3.10.2.3 Generations per selective sweep

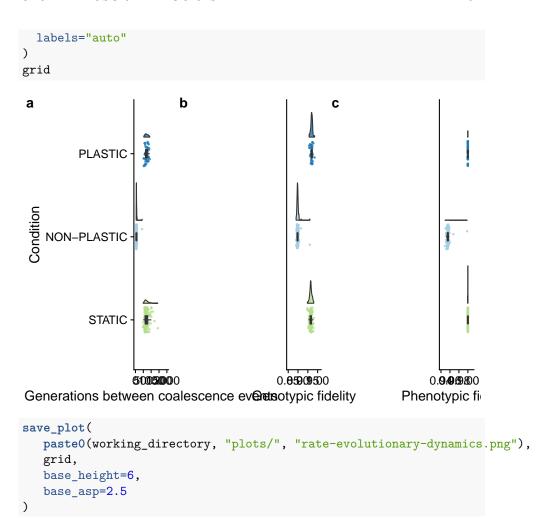
```
selective_sweeps_rate_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=generations_per_mrca_change, fill=condition)
 ) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
  ) +
  scale_y_continuous(
   name="Generations between coalescence events",
   limits=c(0, 2000),
   breaks=seq(0, 2000, 500)
  ) +
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
  theme(
   legend.position="none"
 ) +
   paste0(working_directory, "plots/", "generations-between-selective-sweeps.png"),
   width=4,
   height=4
```





#### **3.10.2.4** Combined

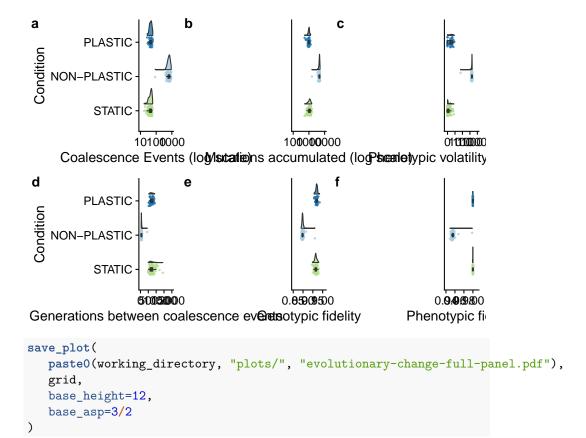
```
grid <- plot_grid(</pre>
  selective_sweeps_rate_fig + theme(
    legend.position="none"
  genotypic_fidelity_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
    axis.title.y=element_blank()
  ),
  phenotypic_fidelity_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
    axis.title.y=element_blank()
  ),
  nrow=1,
  align="v",
```



#### 3.10.3 Full panel

```
grid <- plot_grid(
    selective_sweeps_fig + theme(
        legend.position="none"
),
    mutation_count_fig + theme(
        legend.position="none",
        axis.ticks.y=element_blank(),
        axis.text.y=element_blank(),
        axis.title.y=element_blank()
),
    phenotypic_volatility_fig + theme(</pre>
```

```
legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
    axis.title.y=element_blank()
  ),
  selective_sweeps_rate_fig + theme(
    legend.position="none"
  ),
  genotypic_fidelity_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
    axis.text.y=element_blank(),
   axis.title.y=element_blank()
  ),
  phenotypic_fidelity_fig + theme(
    legend.position="none",
    axis.ticks.y=element_blank(),
   axis.text.y=element_blank(),
   axis.title.y=element_blank()
  ),
  nrow=2,
  ncol=3,
  align="v",
 labels="auto"
grid
```



### Chapter 4

# Evolution and maintenance of novel traits

The effect of adaptive phenotypic plasticity on the evolution and maintenance of novel tasks.

#### 4.1 Overview

```
total_updates <- 200000
replicates <- 100
focal_traits <- c("not", "nand", "and", "ornot", "or", "andnot")</pre>
traits_set_a <- c("not", "and", "or")</pre>
traits_set_b <- c("nand", "ornot", "andnot")</pre>
extra_traits <- c(</pre>
  "nor", "xor", "equals",
  "logic_3aa", "logic_3ab", "logic_3ac",
  "logic_3ad", "logic_3ae", "logic_3af",
  "logic_3ag", "logic_3ah", "logic_3ai",
  "logic_3aj", "logic_3ak", "logic_3al",
  "logic_3am", "logic_3an", "logic_3ao",
  "logic_3ap", "logic_3aq", "logic_3ar",
  "logic_3as", "logic_3at", "logic_3au",
  "logic_3av", "logic_3aw", "logic_3ax",
  "logic_3ay", "logic_3az", "logic_3ba",
  "logic_3bb","logic_3bc","logic_3bd",
  "logic_3be", "logic_3bf", "logic_3bg",
  "logic_3bh", "logic_3bi", "logic_3bj",
  "logic_3bk", "logic_3b1", "logic_3bm",
```

```
"logic_3bn", "logic_3bo", "logic_3bp",
    "logic_3bq", "logic_3br", "logic_3bs",
    "logic_3bt", "logic_3bu", "logic_3bv",
    "logic_3bw", "logic_3bx", "logic_3by",
    "logic_3bz", "logic_3ca", "logic_3cb",
    "logic_3cc", "logic_3cd", "logic_3ce",
    "logic_3cf", "logic_3cg", "logic_3ch",
    "logic_3ci", "logic_3cj", "logic_3ck",
    "logic_3cl", "logic_3cm", "logic_3cn",
    "logic_3co", "logic_3cp"
)

# Relative location of data.
working_directory <- "experiments/2021-01-31-complex-features/analysis/" # << For book
# working_directory <- "./"</pre>
```

#### 4.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
library(RColorBrewer)
library(Hmisc)
library(boot)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd9")
```

These analyses were conducted/knitted with the following computing environment:

```
print(version)
## platform
                  x86_64-pc-linux-gnu
## arch
                  x86_64
## os
                  linux-gnu
## system
                  x86_64, linux-gnu
## status
                  4
## major
## minor
                  0.4
                  2021
## year
## month
                  02
## day
                  15
                  80002
## svn rev
## language
```

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#### 4.3 Setup

```
###### summary data ######
summary_data_loc <- paste0(working_directory, "data/aggregate.csv")</pre>
summary_data <- read.csv(summary_data_loc, na.strings="NONE")</pre>
summary_data$DISABLE_REACTION_SENSORS <- as.factor(summary_data$DISABLE_REACTION_SENSORS)</pre>
summary_data$chg_env <- summary_data$chg_env == "True"</pre>
summary_data$dominant_plastic_odd_even <- as.factor(summary_data$dominant_plastic_odd_even)</pre>
summary_data$sensors <- summary_data$DISABLE_REACTION_SENSORS == "0"</pre>
summary_data$is_plastic <- summary_data$dominant_plastic_odd_even == "True"</pre>
summary_data$extra_task_value <- as.factor(summary_data$extra_task_value)</pre>
summary_data <- filter(summary_data, extra_task_value == 0.1)</pre>
env_label_fun <- function(chg_env) {</pre>
  if (chg_env) {
    return("Fluctuating")
  } else {
    return("Constant")
  }
}
sensors label fun <- function(has sensors) {</pre>
  if (has_sensors) {
   return("Sensors")
  } else {
    return("No sensors")
  }
}
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
  } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
}
summary_data$env_label <- mapply(</pre>
```

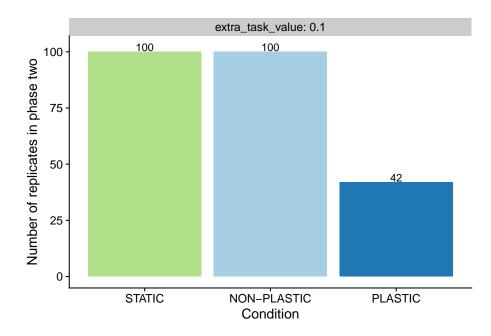
```
env_label_fun,
  summary_data$chg_env
summary_data$sensors_label <- mapply(</pre>
 sensors_label_fun,
 summary_data$sensors
summary_data$condition <- mapply(</pre>
 condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
condition_order = c(
  "STATIC",
  "NON-PLASTIC",
 "PLASTIC"
)
##### time series ####
lineage_time_series_data_loc <- pasteO(working_directory, "data/lineage_series.csv")</pre>
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_date</pre>
lineage_time_series_data$chg_env <- lineage_time_series_data$chg_env == "True"</pre>
lineage_time_series_data$sensors <- lineage_time_series_data$DISABLE_REACTION_SENSORS
lineage_time_series_data$extra_task_value <- as.factor(lineage_time_series_data$extra_</pre>
lineage_time_series_data$env_label <- mapply(</pre>
  env_label_fun,
  lineage_time_series_data$chg_env
lineage_time_series_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
 lineage_time_series_data$sensors
lineage_time_series_data$condition <- mapply(</pre>
 condition_label_fun,
 lineage_time_series_data$sensors,
 lineage_time_series_data$chg_env
)
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
```

```
# Create directory to dump plots
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
# Sample mean function
samplemean <- function(x, d) {
   return(mean(x[d]))
}</pre>
```

#### 4.4 The evolution of phenotypic plasticity

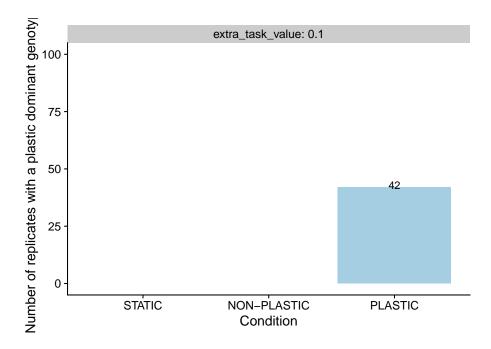
For sensor-enabled populations in fluctuating environments, we only transfered populations containing an optimally plastic genotype to phase two.

```
summary_data_grouped = dplyr::group_by(summary_data, sensors, env_label, condition, extra_task_va
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
  geom_col(position=position_dodge(0.9)) +
  geom_text(aes(label=n, y=n+2)) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ylab("Number of replicates in phase two") +
  facet_wrap(~extra_task_value, labeller=label_both) +
  theme(
   legend.position="none"
```



We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

```
summary_data_grouped = dplyr::group_by(summary_data, condition, is_plastic, extra_task
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condi-
  geom_col(position=position_dodge(0.9)) +
  scale_x_discrete(
    name="Condition",
   limits=condition_order
  ) +
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
    palette="Paired"
 ylim(0, 100) +
  geom_text(aes(label=n, y=n+1)) +
 ylab("Number of replicates with a plastic dominant genotype") +
 facet_wrap(~extra_task_value, labeller=label_both) +
  theme(
    legend.position="none"
```

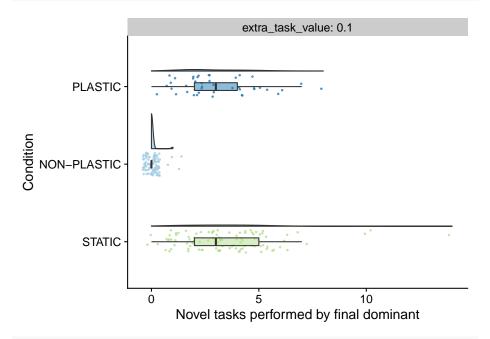


## 4.5 Novel task performance - final dominant genotype

How many novel tasks do final dominant genotypes perform?

```
ggplot(summary_data, aes(x=condition, y=dominant_extra_tasks, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
```

```
) +
 ylab("Novel tasks performed by final dominant") +
  scale_fill_brewer(
   palette="Paired"
 ) +
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
 facet_wrap(
   ~extra_task_value,
   labeller=label_both
 ) +
 theme(
    legend.position="none"
  ) +
 ggsave(
    pasteO(working_directory, "plots/dominant-extra-tasks.pdf"),
    width=15,
    height=10
 )
```



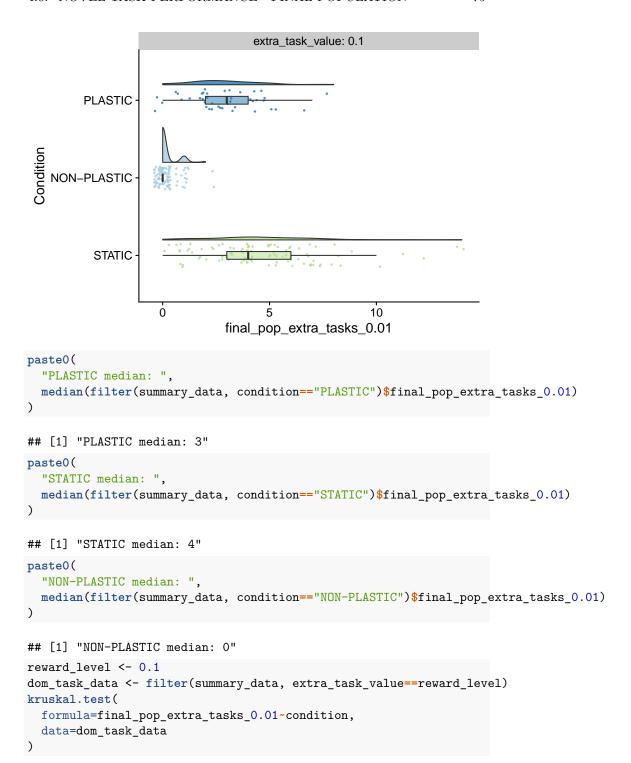
```
paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_extra_tasks)
```

```
## [1] "PLASTIC median: 3"
paste0(
 "STATIC median: ",
 median(filter(summary_data, condition=="STATIC")$dominant_extra_tasks)
## [1] "STATIC median: 3"
paste0(
 "NON-PLASTIC median: ",
 median(filter(summary_data, condition=="NON-PLASTIC")$dominant_extra_tasks)
## [1] "NON-PLASTIC median: 0"
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
 formula=dominant_extra_tasks~condition,
 data=dom_task_data
)
## Kruskal-Wallis rank sum test
## data: dominant_extra_tasks by condition
## Kruskal-Wallis chi-squared = 177.17, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=dom_task_data$dominant_extra_tasks,
  g=dom_task_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: dom_task_data$dominant_extra_tasks and dom_task_data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.9
## P value adjustment method: bonferroni
```

# 4.6 Novel task performance - final population

How many novel tasks are performed across the final population (1% of organisms must perform to count)?

```
ggplot(summary_data, aes(x=condition, y=final_pop_extra_tasks_0.01, fill=condition)) +
 geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
    palette="Paired"
  scale_color_brewer(
   palette="Paired"
  coord_flip() +
 facet_wrap(
    ~extra_task_value,
   labeller=label both
 ) +
 theme(
    legend.position="none"
```

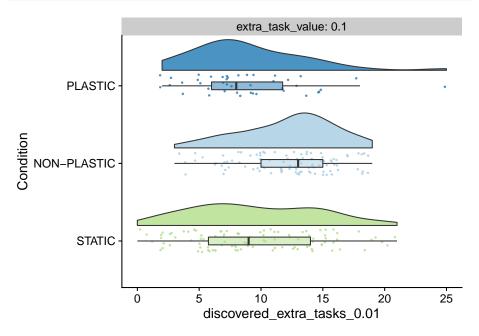


```
##
##
   Kruskal-Wallis rank sum test
##
## data: final_pop_extra_tasks_0.01 by condition
## Kruskal-Wallis chi-squared = 169.47, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=dom_task_data$final_pop_extra_tasks_0.01,
 g=dom_task_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: dom_task_data$final_pop_extra_tasks_0.01 and dom_task_data$condition
##
           NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       0.00016
##
## P value adjustment method: bonferroni
```

## 4.7 Novel task discovery - population

```
ggplot(summary_data, aes(x=condition, y=discovered_extra_tasks_0.01, fill=condition))
 geom_flat_violin(
    position = position nudge(x = .2, y = 0),
    alpha = .8
 ) +
  geom_point(
    mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  geom_boxplot(
   width = .1,
    outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
```

```
limits=condition_order
) +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
facet_wrap(
   ~extra_task_value,
   labeller=label_both
) +
theme(
   legend.position="none"
)
```

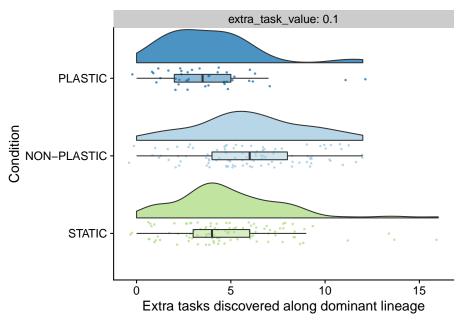


```
paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$discovered_extra_tasks_0.01)
)
## [1] "PLASTIC median: 8"
paste0(
   "STATIC median: ",
```

```
median(filter(summary_data, condition=="STATIC")$discovered_extra_tasks_0.01)
## [1] "STATIC median: 9"
paste0(
 "NON-PLASTIC median: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$discovered_extra_tasks_0.01)
)
## [1] "NON-PLASTIC median: 13"
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
  formula=discovered_extra_tasks_0.01~condition,
  data=dom_task_data
##
##
   Kruskal-Wallis rank sum test
##
## data: discovered_extra_tasks_0.01 by condition
## Kruskal-Wallis chi-squared = 24.271, df = 2, p-value = 5.365e-06
pairwise.wilcox.test(
  x=dom_task_data$discovered_extra_tasks_0.01,
  g=dom_task_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: dom_task_data$discovered_extra_tasks_0.01 and dom_task_data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 2.4e-05
## STATIC 0.00035
                       1.00000
## P value adjustment method: bonferroni
```

# 4.8 Novel task discovery - lineage of final dominant genotype

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_discovered, fill=condition)
  geom flat violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition order
  ylab("Extra tasks discovered along dominant lineage") +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
  facet_wrap(
    ~extra_task_value,
   labeller=label_both
  ) +
  theme(
   legend.position="none"
  ggsave(
   paste0(working_directory, "plots/dominant-lineage-extra-tasks-discovered.pdf"),
   width=15,
   height=10
```



```
paste0(
  "PLASTIC median: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_disc
## [1] "PLASTIC median: 3.5"
paste0(
  "STATIC median: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_disco-
)
## [1] "STATIC median: 4"
paste0(
  "NON-PLASTIC median: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_
## [1] "NON-PLASTIC median: 6"
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
  formula=dominant_lineage_extra_traits_discovered~condition,
  data=dom_task_data
```

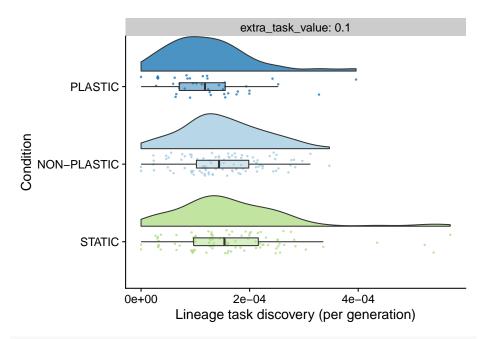
```
##
   Kruskal-Wallis rank sum test
##
##
## data: dominant_lineage_extra_traits_discovered by condition
## Kruskal-Wallis chi-squared = 24.099, df = 2, p-value = 5.846e-06
pairwise.wilcox.test(
  x=dom_task_data$dominant_lineage_extra_traits_discovered,
  g=dom_task_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: dom_task_data$dominant_lineage_extra_traits_discovered and dom_task_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC 1.7e-05
## STATIC 0.0035
                       0.0561
##
## P value adjustment method: bonferroni
```

# 4.8.1 Per-generation novel task discovery - lineage of final dominant genotype

```
summary_data$dominant_lineage_extra_traits_discovered_per_generation <- summary_data$dominant_lineage_extra_traits_discovered_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_generation_per_gener
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_discovered_per_generation,
          geom_flat_violin(
                    position = position_nudge(x = .2, y = 0),
                     alpha = .8
          ) +
          geom_point(
                    mapping=aes(color=condition),
                    position = position_jitter(width = .15),
                    size = .5,
                    alpha = 0.8
          ) +
          geom_boxplot(
                    width = .1,
                    outlier.shape = NA,
                    alpha = 0.5
          scale_x_discrete(
```

```
name="Condition",
  limits=condition_order
) +
ylab("Lineage task discovery (per generation)") +
facet_wrap(
  ~extra_task_value,
 labeller=label_both
) +
scale_fill_brewer(
 palette="Paired"
scale_color_brewer(
  palette="Paired"
) +
coord_flip() +
theme(
 legend.position="none"
ggsave(paste0(working_directory, "plots/", "discovery-per-generation.png"))
```

#### ## Saving $6.5 \times 4.5$ in image

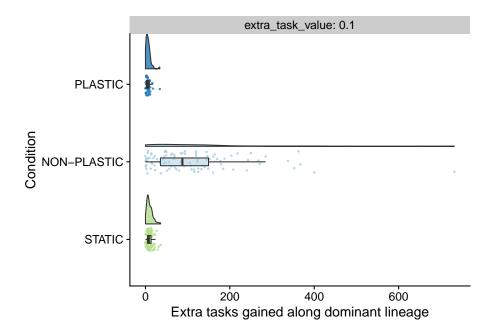


```
paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_disc.
```

```
## [1] "PLASTIC median: 0.000117695011124939"
paste0(
 "STATIC median: ",
 median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_discovered_per_g
## [1] "STATIC median: 0.00015363220504867"
paste0(
  "NON-PLASTIC median: ",
 median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_discovered
)
## [1] "NON-PLASTIC median: 0.00014358046266055"
reward level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
 formula=dominant_lineage_extra_traits_discovered_per_generation~condition,
 data=dom_task_data
)
## Kruskal-Wallis rank sum test
## data: dominant_lineage_extra_traits_discovered_per_generation by condition
## Kruskal-Wallis chi-squared = 7.1465, df = 2, p-value = 0.02806
pairwise.wilcox.test(
 x=dom_task_data$dominant_lineage_extra_traits_discovered_per_generation,
  g=dom_task_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: dom_task_data$dominant_lineage_extra_traits_discovered_per_generation and dom_task_data
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 0.092
                       0.025
## STATIC 1.000
## P value adjustment method: bonferroni
```

# 4.9 Novel tasks gained along final dominant lineages

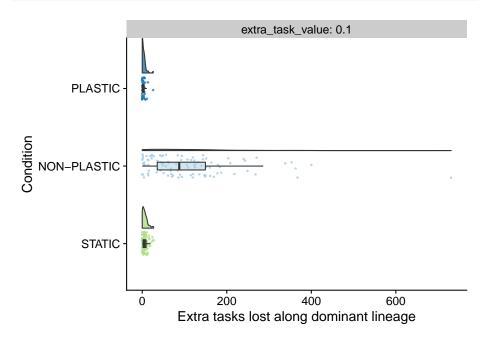
```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_gained, fill=condition)
  geom flat violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
 geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
 geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
 scale_x_discrete(
   name="Condition",
   limits=condition order
 ) +
 ylab("Extra tasks gained along dominant lineage") +
  scale_fill_brewer(
   palette="Paired"
 ) +
 scale_color_brewer(
    palette="Paired"
  coord_flip() +
 facet_wrap(
    ~extra_task_value,
   labeller=label_both
 ) +
 theme(
    legend.position="none"
 ggsave(
   paste0(working_directory, "plots/dominant-lineage-extra-tasks-gained.pdf"),
    width=15,
    height=10
```



# 4.10 Novel task loss along final dominant lineages

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_lost, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
```

```
ylab("Extra tasks lost along dominant lineage") +
scale_fill_brewer(
 palette="Paired"
) +
scale_color_brewer(
  palette="Paired"
) +
coord_flip() +
facet_wrap(
  ~extra_task_value,
 labeller=label_both
) +
theme(
  legend.position="none"
) +
ggsave(
  paste0(working_directory, "plots/dominant-lineage-extra-tasks-lost.pdf"),
  width=15,
  height=10
)
```



```
paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_lost
)
```

```
## [1] "PLASTIC median: 2"
paste0(
  "STATIC median: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_lost)
## [1] "STATIC median: 5"
paste0(
 "NON-PLASTIC median: ",
 median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_lost)
)
## [1] "NON-PLASTIC median: 87.5"
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
  formula=dominant_lineage_extra_traits_lost~condition,
  data=dom_task_data
)
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_extra_traits_lost by condition
## Kruskal-Wallis chi-squared = 129.06, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=dom_task_data$dominant_lineage_extra_traits_lost,
  g=dom_task_data$condition,
 p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: dom_task_data$dominant_lineage_extra_traits_lost and dom_task_data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 2.7e-16
                       0.0024
## STATIC < 2e-16
## P value adjustment method: bonferroni
```

```
summary_data$dominant_lineage_extra_traits_lost_per_generation <- summary_data$dominan
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_lost_per_generat
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ylab("Extra tasks lost along dominant lineage (per generation)") +
 facet_wrap(
    ~extra_task_value,
   labeller=label_both
  scale fill brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
 ) +
 coord_flip() +
 theme(
   legend.position="none"
 ggsave(paste0(working_directory, "plots/", "tasks-lost-per-generation.png"))
```

```
extra_task_value: 0.1
 Condition
   NON-PLASTIC
          STATIC
                 0.000
                               0.005
                                            0.010
                                                          0.015
                 Extra tasks lost along dominant lineage (per generation)
paste0(
  "PLASTIC median: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_lost_per_general
## [1] "PLASTIC median: 6.25141973661864e-05"
paste0(
  "STATIC median: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_lost_per_generat
)
## [1] "STATIC median: 0.000161396283669756"
paste0(
  "NON-PLASTIC median: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_lost_per_ge
## [1] "NON-PLASTIC median: 0.0022026054610079"
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
  formula=dominant_lineage_extra_traits_lost_per_generation~condition,
  data=dom\_task\_data
```

```
##
   Kruskal-Wallis rank sum test
##
##
## data: dominant_lineage_extra_traits_lost_per_generation by condition
## Kruskal-Wallis chi-squared = 121.41, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=dom_task_data$dominant_lineage_extra_traits_lost_per_generation,
  g=dom_task_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: dom_task_data$dominant_lineage_extra_traits_lost_per_generation and dom_task
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 1.1e-15
## STATIC < 2e-16
                       0.0012
##
## P value adjustment method: bonferroni
```

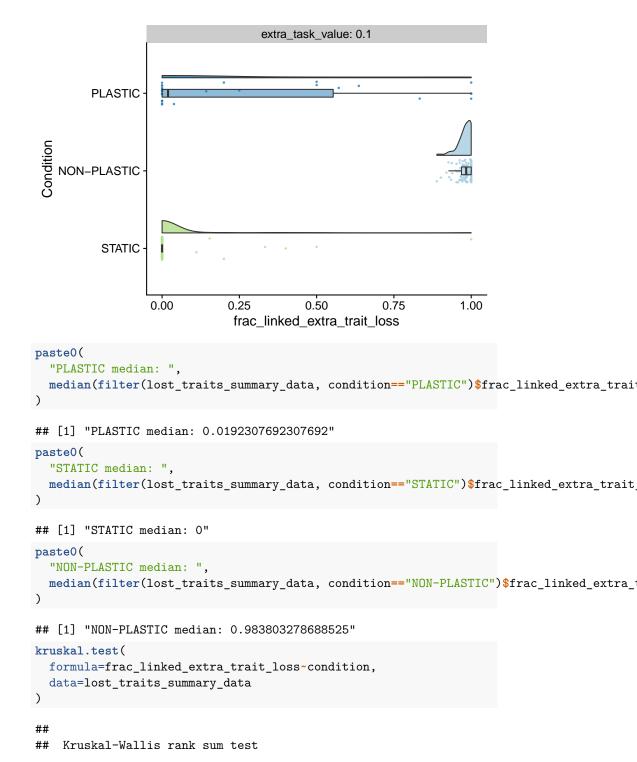
# 4.11 How many instances of novel trait loss cooccurred with changes in base phenotype?

Task loss linked with primary trait changes.

scale\_color\_brewer(

```
lost_traits_summary_data <- filter(summary_data, extra_task_value==0.1 & dominant_line
lost_traits_summary_data$frac_linked_extra_trait_loss <- lost_traits_summary_data$domi:
# ggplot(lost_traits_summary_data, aes(x=frac_linked_extra_trait_loss, fill=condition)
   geom_density() +
#
   facet_grid(
     condition~extra_task_value,
#
     labeller=label_both
   ) +
   theme(
     legend.position="none"
   ) +
#
   scale_fill_brewer(
    palette="Paired"
```

```
#
     palette="Paired"
#
  ) +
#
   ggsave(
     pasteO(working_directory, "plots/dominant-lineage-extra-tasks-lost-linkage.png"),
#
#
      width=15,
#
      height=10
ggplot(lost_traits_summary_data, aes(x=condition, y=frac_linked_extra_trait_loss, fill=condition)
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  ) +
  coord_flip() +
  facet_wrap(
   ~extra_task_value,
   labeller=label_both
  ) +
  theme(
   legend.position="none"
```



```
##
## data: frac_linked_extra_trait_loss by condition
## Kruskal-Wallis chi-squared = 153.68, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=lost_traits_summary_data$frac_linked_extra_trait_loss,
  g=lost_traits_summary_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: lost_traits_summary_data$frac_linked_extra_trait_loss and lost_traits_summary_data$cond
           NON-PLASTIC PLASTIC
##
## PLASTIC 1.9e-08
## STATIC < 2e-16
                       1.8e-06
## P value adjustment method: bonferroni
sum(filter(lost_traits_summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_lost
## [1] 10998
sum(filter(lost_traits_summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_lost
## [1] 11229
aggregate_frac_linked_extra_trait_loss_nonplastic <- sum(filter(lost_traits_summary_data, condition))
aggregate_frac_linked_extra_trait_loss_nonplastic
## [1] 0.9794283
sum(filter(lost_traits_summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_lost_lineage
## [1] 29
sum(filter(lost_traits_summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_lost)
## [1] 142
aggregate_frac_linked_extra_trait_loss_plastic <- sum(filter(lost_traits_summary_data, condition=
aggregate_frac_linked_extra_trait_loss_plastic
## [1] 0.2042254
sum(filter(lost_traits_summary_data, condition=="STATIC")$dominant_lineage_extra_traits_lost_link
## [1] 13
```

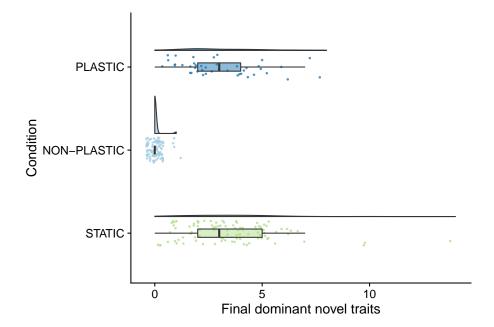
```
sum(filter(lost_traits_summary_data, condition=="STATIC")$dominant_lineage_extra_trait
## [1] 631
aggregate_frac_linked_extra_trait_loss_nonplastic <- sum(filter(lost_traits_summary_data))
aggregate_frac_linked_extra_trait_loss_nonplastic
## [1] 0.02060222</pre>
```

## 4.12 Manuscript figures

#### 4.12.1 Overall task performance

```
extra_task_reward_value=0.1
dominant_extra_tasks_fig <- ggplot(</pre>
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_extra_tasks, fill=condition)
 ) +
 geom flat violin(
   position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  ) +
 geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
 ) +
  scale_x_discrete(
    name="Condition",
   limits=condition_order,
   labels=condition_order
  scale_y_continuous(
   name="Final dominant novel traits"
 ) +
 scale fill brewer(
   palette="Paired"
 ) +
 scale_color_brewer(
```

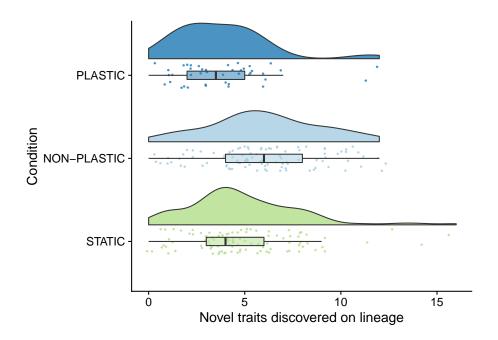
```
palette="Paired"
) +
theme(
  legend.position="none"
) +
coord_flip()
dominant_extra_tasks_fig
```



#### 4.12.2 Overall task discovery

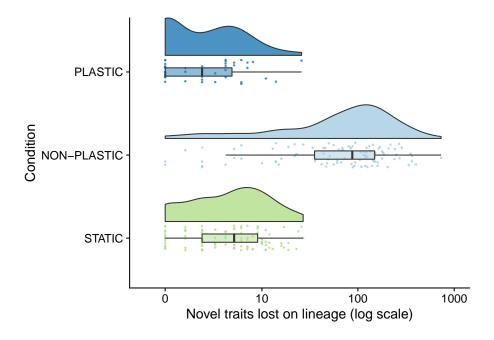
```
lineage_extra_tasks_discovered_fig <- ggplot(
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_lineage_extra_traits_discovered, fill=condition)
) +
    geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
    geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
) +</pre>
```

```
geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
    name="Condition",
    limits=condition_order,
    {\tt labels=condition\_order}
  scale_y_continuous(
    name="Novel traits discovered on lineage"
  ) +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
    palette="Paired"
  theme(
    legend.position="none"
  ) +
  coord_flip()
lineage_extra_tasks_discovered_fig
```



#### 4.12.3 Overall task loss

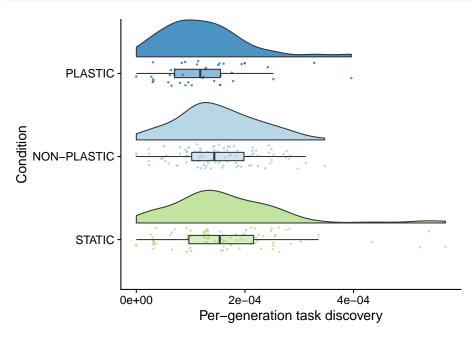
```
lineage_extra_tasks_lost_fig <- ggplot(</pre>
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_lineage_extra_traits_lost, fill=condition)
  geom flat violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 ) +
  scale_y_continuous(
   name="Novel traits lost on lineage (log scale)",
   trans="pseudo_log",
   breaks=c(0,10,100,1000),
   limits=c(-1,1000)
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  ) +
  theme(
   legend.position="none"
  ) +
  coord_flip()
lineage_extra_tasks_lost_fig
```



#### 4.12.4 Per-generation task discovery

```
lineage_per_gen_task_discovery <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_extra_traits_discovered_per_generation, fill=c
  ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  scale_x_discrete(
    name="Condition",
    limits=condition_order
```

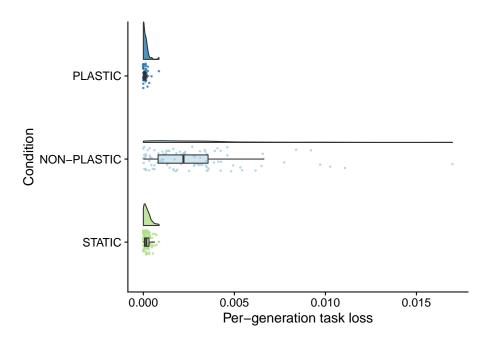
```
) +
ylab("Per-generation task discovery") +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
)
lineage_per_gen_task_discovery
```



#### 4.12.5 Per-generation task loss

```
lineage_per_gen_task_loss <- ggplot(
    summary_data,
    aes(x=condition, y=dominant_lineage_extra_traits_lost_per_generation, fill=condition)
) +
geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +</pre>
```

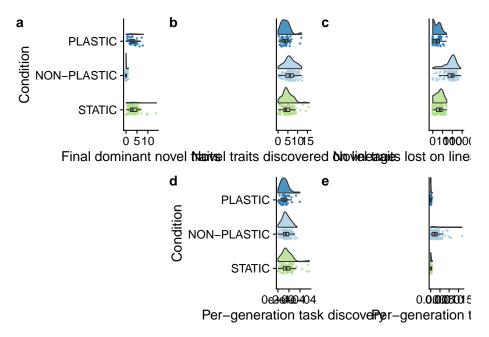
```
geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  ylab("Per-generation task loss") +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
    palette="Paired"
  ) +
  coord_flip() +
 theme(
   legend.position="none"
lineage_per_gen_task_loss
```



#### 4.13 Combined panel

```
grid <- plot_grid(</pre>
 dominant_extra_tasks_fig,
  lineage_extra_tasks_discovered_fig + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank()
 lineage_extra_tasks_lost_fig + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank(),a
  lineage_per_gen_task_discovery,
 lineage_per_gen_task_loss + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank(),axis
 nrow=2,
  align="v",
  # labels="auto"
 labels=c("a", "b","c","", "d","e")
)
save_plot(
  pasteO(working_directory, "plots/", "complex-traits-panel.pdf"),
   grid,
   base_height=12,
   base_asp=3/2
)
grid
```

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```
# save_plot(
#     pasteO(working_directory, "plots/", "complex-traits-panel.png"),
#     grid,
#     base_height=6,
#     base_asp=2.5
# )
```

# Chapter 5

# Accumulation of deleterious instructions

The effect of adaptive phenotypic plasticity on the accumulation of deleterious genes.

#### 5.1 Overview

```
total_updates <- 200000
replicates <- 100

focal_traits <- c("not", "nand", "and", "ornot", "or", "andnot")
traits_set_a <- c("not", "and", "or")
traits_set_b <- c("nand", "ornot", "andnot")

# Relative location of data.
working_directory <- "experiments/2021-02-05-hitchhiking/analysis/" # << For bookdown
# working_directory <- "./"</pre>
```

## 5.2 Analysis dependencies

Load all required R libraries.

```
library(RColorBrewer)
library(ggplot2)
library(tidyverse)
library(cowplot)
library(Hmisc)
```

```
library(boot)
library(fmsb)
library(knitr)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd9
These analyses were conducted/knitted with the following computing environment:
print(version)
```

```
##
## platform
                  x86_64-pc-linux-gnu
## arch
                  x86 64
## os
                  linux-gnu
## system
                  x86_64, linux-gnu
## status
## major
                  0.4
## minor
                  2021
## year
## month
                  02
## day
                  15
## svn rev
                  80002
## language
                  R
## version.string R version 4.0.4 (2021-02-15)
## nickname
                 Lost Library Book
```

### 5.3 Setup

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```
sensors_label_fun <- function(has_sensors) {</pre>
  if (has_sensors) {
    return("Sensors")
 } else {
    return("No sensors")
  }
}
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
 } else if (env_chg) {
    return("NON-PLASTIC")
 } else {
    return("STATIC")
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
summary_data$condition <- mapply(</pre>
  condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
condition_order = c(
  "STATIC",
  "NON-PLASTIC",
  "PLASTIC"
)
##### time series ####
lineage_time_series_data_loc <- paste0(working_directory, "data/lineage_series.csv")</pre>
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_data$DISABLE_I
```

```
lineage_time_series_data$chg_env <- lineage_time_series_data$chg_env == "True"</pre>
lineage_time_series_data$sensors <- lineage_time_series_data$DISABLE_REACTION_SENSORS
lineage_time_series_data$POISON_PENALTY <- as.factor(lineage_time_series_data$POISON_V</pre>
lineage_time_series_data$env_label <- mapply(</pre>
  env_label_fun,
  lineage_time_series_data$chg_env
lineage_time_series_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
 lineage_time_series_data$sensors
lineage_time_series_data$condition <- mapply(</pre>
  condition_label_fun,
  lineage_time_series_data$sensors,
  lineage_time_series_data$chg_env
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
samplemean <- function(x, d) {</pre>
 return(mean(x[d]))
}
```

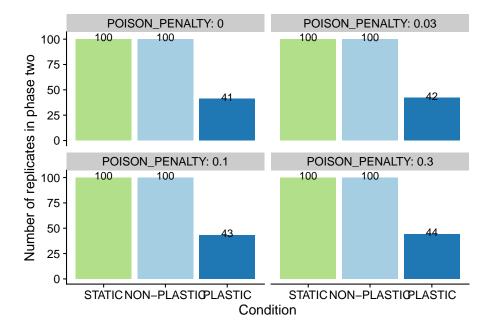
## 5.4 Evolution of phenotypic plasticity

For sensor-enabled populations in fluctuating environments, we only transferred populations containing an optimally plastic genotype to phase-two.

```
summary_data_grouped = dplyr::group_by(summary_data, sensors, env_label, condition, PO
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())

ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    geom_text(aes(label=n, y=n+2)) +
    scale_x_discrete(
    name="Condition",
    limits=condition_order
) +
    scale_fill_brewer(
    palette="Paired"
) +
    scale_color_brewer(
```

```
palette="Paired"
) +
ylab("Number of replicates in phase two") +
facet_wrap(~POISON_PENALTY, labeller=label_both) +
theme(
  legend.position="none"
)
```

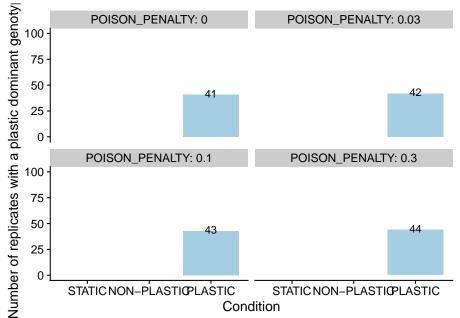


We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

```
summary_data_grouped = dplyr::group_by(summary_data, condition, is_plastic, POISON_PENALTY)
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
```

```
## `summarise()` has grouped output by 'condition', 'is_plastic'. You can override using the `.gr
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    geom_text(aes(label=n, y=n+1)) +
    scale_fill_brewer(
        palette="Paired"
) +
```

```
scale_color_brewer(
   palette="Paired"
) +
ylab("Number of replicates with a plastic dominant genotype") +
ylim(0, 100) +
facet_wrap(~POISON_PENALTY, labeller=label_both) +
theme(
   legend.position="none"
)
```



#### 5.5 Poison instruction execution

# 5.5.1 Number of replicates where final dominant genotype executes the poison instruction

```
poison_penalty <- 0.1

occurrences <- c(
  length(filter(summary_data, POISON_PENALTY==poison_penalty & condition=="NON-PLASTIC length(filter(summary_data, POISON_PENALTY==poison_penalty & condition=="PLASTIC" & description of the condition of the conditio
```

```
length(filter(summary_data, POISON_PENALTY==poison_penalty & condition=="PLASTIC")$RANDOM_SEED)
  length(filter(summary_data, POISON_PENALTY==poison_penalty & condition=="STATIC" )$RANDOM_SEED)
names(trials) <- c(</pre>
  "NON-PLASTIC",
  "PLASTIC",
  "STATIC"
)
names(occurrences) <- c(</pre>
 "NON-PLASTIC",
  "PLASTIC",
  "STATIC"
)
poison_exec_table <- data.frame(</pre>
  executes.poison=occurrences,
 replicates=trials
kable(poison_exec_table)
```

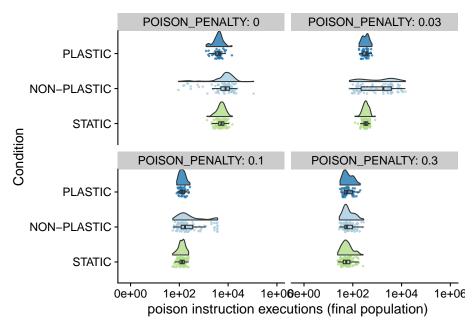
	executes.poison	replicates
NON-PLASTIC	14	100
PLASTIC	0	43
STATIC	0	100

```
pairwise.fisher.test(x=occurrences, n=trials, p.adjust.method="bonferroni")
##
## Pairwise comparisons using Pairwise comparison of proportions (Fisher)
##
## data: occurrences out of trials
##
## NON-PLASTIC PLASTIC
## PLASTIC 0.03212 -
## STATIC 0.00022 1.00000
##
## P value adjustment method: bonferroni
```

#### 5.5.2 Poison instruction execution in final population

```
ggplot(summary_data, aes(x=condition, y=final_population_poison, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
  geom_point(
```

```
mapping=aes(color=condition),
  position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
 width = .1,
  outlier.shape = NA,
  alpha = 0.5
) +
scale_x_discrete(
 name="Condition",
 limits=condition_order
scale_y_continuous(
 name="poison instruction executions (final population)",
  trans="pseudo_log",
 breaks=c(0,100,10000,1000000),
 limits=c(-1,1000000)
) +
scale_fill_brewer(
 palette="Paired"
) +
scale_color_brewer(
 palette="Paired"
facet_wrap(
  ~POISON_PENALTY,
  labeller=label both
) +
coord_flip() +
theme(
 legend.position="none"
) +
ggsave(
 pasteO(working_directory, "plots/final-population-poison-log.pdf"),
 width=15,
 height=10
```



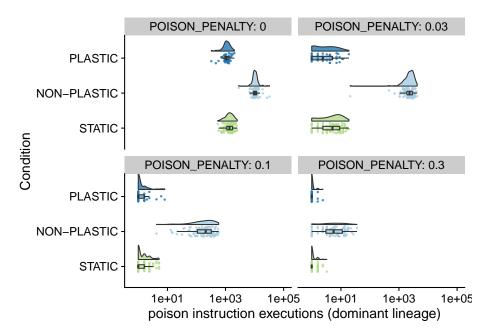
```
penalties <- levels(summary_data$POISON_PENALTY)</pre>
for (penalty in penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)</pre>
 print(
    paste0(
      "PENALTY: ", penalty
  kt <- kruskal.test(</pre>
      formula=final_population_poison~condition,
      data=stat_data
    )
 print(
    kt
  if (is.na(kt$p.value)) { next }
  if (kt$p.value > 0.05) { next }
  print(
    pairwise.wilcox.test(
      x=stat_data$final_population_poison,
      g=stat_data$condition,
      p.adjust.method="bonferroni"
    )
}
```

```
## [1] "PENALTY: O"
##
## Kruskal-Wallis rank sum test
##
## data: final_population_poison by condition
## Kruskal-Wallis chi-squared = 43.589, df = 2, p-value = 3.426e-10
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$final_population_poison and stat_data$condition
##
          NON-PLASTIC PLASTIC
## PLASTIC 8.7e-07
## STATIC 9.8e-07
                     0.00074
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
##
## Kruskal-Wallis rank sum test
##
## data: final_population_poison by condition
## Kruskal-Wallis chi-squared = 20.74, df = 2, p-value = 3.136e-05
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$final_population_poison and stat_data$condition
##
          NON-PLASTIC PLASTIC
##
## PLASTIC 0.003
## STATIC 1e-04
                      1.000
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
## Kruskal-Wallis rank sum test
##
## data: final_population_poison by condition
## Kruskal-Wallis chi-squared = 20.608, df = 2, p-value = 3.35e-05
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$final_population_poison and stat_data$condition
##
```

# 5.5.3 Poison instruction execution along final dominant lineage (cumulative)

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_times_poison_executed, fill=condition))
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  scale_y_continuous(
   name="poison instruction executions (dominant lineage)",
   trans="pseudo_log",
   breaks=c(10,1000,100000),
   limits=c(-1,100000)
  ) +
  facet_wrap(
    ~POISON PENALTY,
   labeller=label_both
```

```
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
) +
ggsave(
   paste0(working_directory, "plots/final-dominant-lineage-poison-log.pdf"),
   width=15,
   height=10
)
```



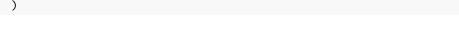
```
penalties <- levels(summary_data$POISON_PENALTY)
for (penalty in penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)
  print(
    pasteO(
        "PENALTY: ", penalty
    )
  )
  kt <- kruskal.test(</pre>
```

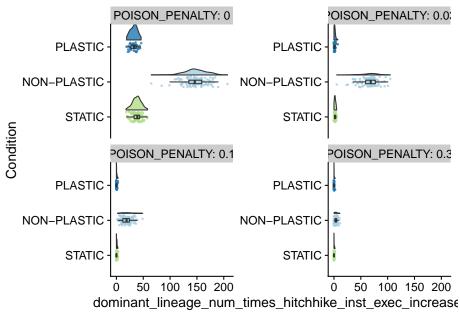
```
formula=dominant_lineage_times_poison_executed~condition,
      data=stat_data
   )
 print(
   kt
  if (is.na(kt$p.value)) { next }
  if (kt$p.value > 0.05) { next }
 print(
   pairwise.wilcox.test(
     x=stat_data$dominant_lineage_times_poison_executed,
      g=stat_data$condition,
     p.adjust.method="bonferroni"
   )
  )
}
## [1] "PENALTY: O"
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_times_poison_executed by condition
## Kruskal-Wallis chi-squared = 178.84, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_times_poison_executed and stat_data$condition
          NON-PLASTIC PLASTIC
##
## PLASTIC <2e-16
## STATIC <2e-16
                       0.0018
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
##
## Kruskal-Wallis rank sum test
## data: dominant_lineage_times_poison_executed by condition
## Kruskal-Wallis chi-squared = 178.62, df = 2, p-value < 2.2e-16
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_times_poison_executed and stat_data$condition
```

```
##
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                     0.011
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_times_poison_executed by condition
## Kruskal-Wallis chi-squared = 184.83, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_times_poison_executed and stat_data$condition
##
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                      0.21
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.3"
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_times_poison_executed by condition
## Kruskal-Wallis chi-squared = 149.48, df = 2, p-value < 2.2e-16
##
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_times_poison_executed and stat_data$condition
##
          NON-PLASTIC PLASTIC
## PLASTIC 4.4e-16
## STATIC < 2e-16
                      0.84
## P value adjustment method: bonferroni
```

- 5.6 Characterizing mutations that increase poison instruction execution
- 5.6.1 Number of offspring along dominant lineage with increase in poison instruction execution

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases.
  geom flat violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale fill brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
   palette="Paired"
  coord_flip() +
  facet_wrap(
    ~POISON_PENALTY,
   labeller=label_both,
   scales="free_y"
  ) +
  theme(
   legend.position="none"
  ) +
   paste0(working_directory, "plots/final-dominant-lineage-poison-increase-num-mutants-log.png")
   width=15,
   height=10
```





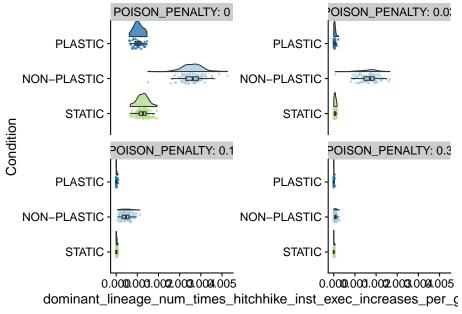
```
penalties <- levels(summary_data$POISON_PENALTY)</pre>
for (penalty in penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)</pre>
  print(
    paste0(
      "PENALTY: ", penalty
  kt <- kruskal.test(</pre>
      formula=dominant_lineage_num_times_hitchhike_inst_exec_increases~condition,
      data=stat_data
  print(
    kt
  if (is.na(kt$p.value)) { next }
  if (kt$p.value > 0.05) { next }
  print(
    pairwise.wilcox.test(
      x=stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases,
      g=stat_data$condition,
      p.adjust.method="bonferroni"
```

```
)
## [1] "PENALTY: O"
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases by condition
## Kruskal-Wallis chi-squared = 179.79, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_data$condit
##
           NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       0.00046
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
## Kruskal-Wallis rank sum test
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases by condition
## Kruskal-Wallis chi-squared = 179.35, df = 2, p-value < 2.2e-16
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_data$condit
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.03
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
##
## Kruskal-Wallis rank sum test
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases by condition
## Kruskal-Wallis chi-squared = 185.34, df = 2, p-value < 2.2e-16
##
##
```

```
Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_o
##
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
                       0.27
## STATIC <2e-16
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.3"
##
##
   Kruskal-Wallis rank sum test
##
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases by condition
## Kruskal-Wallis chi-squared = 146.35, df = 2, p-value < 2.2e-16
##
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_
##
          NON-PLASTIC PLASTIC
##
## PLASTIC 7.8e-16
## STATIC < 2e-16
                       0.86
## P value adjustment method: bonferroni
sum(filter(summary_data, condition=="NON-PLASTIC" & POISON_PENALTY==0.1)$dominant_line
## [1] 1916
sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_:
## [1] 18
sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_lineage_n
## [1] 58
# sum(filter(summary_data, condition=="NON-PLASTIC" & POISON_PENALTY==0.1)$dominant_li
# sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineaq
# sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_lineage
```

# 5.6.2 Per-generation increases in poison instruction execution

```
summary_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation <- summary_data$
ggplot(summary_data, aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  facet_wrap(
    ~POISON_PENALTY,
   labeller=label_both,
   scales="free_y"
  ) +
  coord_flip() +
  theme(
   legend.position="none"
 ) +
   paste0(working_directory, "plots/final-dominant-lineage-poison-increase-per-generation.png");
   width=15,
   height=10
```



```
penalties <- levels(summary_data$POISON_PENALTY)</pre>
for (penalty in penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)</pre>
 print(
    paste0(
      "PENALTY: ", penalty
 kt <- kruskal.test(</pre>
      formula=dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation~
      data=stat_data
    )
 print(
    kt
  )
  if (is.na(kt$p.value)) { next }
  if (kt$p.value > 0.05) { next }
 print(
    pairwise.wilcox.test(
      x=stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generat
      g=stat_data$condition,
      p.adjust.method="bonferroni"
  )
```

}

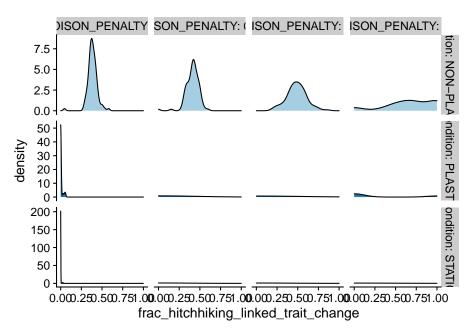
```
## [1] "PENALTY: O"
##
## Kruskal-Wallis rank sum test
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation by condition
## Kruskal-Wallis chi-squared = 180.05, df = 2, p-value < 2.2e-16
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation and a
          NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
                      7.8e-05
## STATIC < 2e-16
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
##
## Kruskal-Wallis rank sum test
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation by condition
## Kruskal-Wallis chi-squared = 176.25, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat data$dominant lineage num times hitchhike inst exec increases per generation and s
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.019
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
## Kruskal-Wallis rank sum test
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation by condition
## Kruskal-Wallis chi-squared = 184.17, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation and a
##
```

```
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.2
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.3"
##
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation by c
## Kruskal-Wallis chi-squared = 140.99, df = 2, p-value < 2.2e-16
##
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_gener
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 2.2e-15
## STATIC < 2e-16
                       0.79
## P value adjustment method: bonferroni
```

# 5.6.3 What fraction of mutations that increase poison instruction execution co-occur with base trait changes?

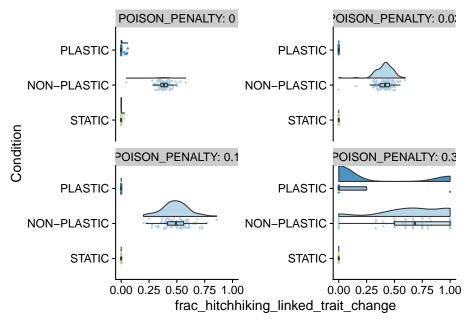
```
summary_data\frac_hitchhiking_linked_trait_change <- summary_data\frac_hitchhiking_trait_change <- summary_data\frac_hitchhiking_trait_change <- summary_data\frac_hitchhiking_trait_change <- summary_data\frac_hitchhiking_trait_change <- summary_data\frac_hitchhiking_trait_change <- summary_data\f
ggplot(filter(summary_data, dominant_lineage_num_times_hitchhike_inst_exec_increases>0
           geom_density() +
           facet_grid(
                         condition~POISON_PENALTY,
                        labeller=label_both,
                         scales="free_y"
           ) +
           scale_fill_brewer(
                       palette="Paired"
           ) +
            scale_color_brewer(
                        palette="Paired"
           ) +
           theme(
                        legend.position="none"
```

```
ggsave(
   paste0(working_directory, "plots/dominant-lineage-frac_hitchhiking_linked_trait_change.png");
   width=15,
   height=10
)
```



```
ggplot(filter(summary_data, dominant_lineage_num_times_hitchhike_inst_exec_increases>0 ), aes(x=o
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
    outlier.shape = NA,
   alpha = 0.5
  scale_x_discrete(
   name="Condition",
   limits=condition_order
```

```
) +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
facet_wrap(
   ~POISON_PENALTY,
   labeller=label_both,
   scales="free_y"
) +
coord_flip() +
theme(
   legend.position="none"
)
```



```
penalties <- levels(summary_data$POISON_PENALTY)
for (penalty in penalties) {
   stat_data <- filter(summary_data, POISON_PENALTY==penalty & dominant_lineage_num_time
   print(
     pasteO(
        "PENALTY: ", penalty
    )
   )
}</pre>
```

```
kt <- kruskal.test(</pre>
     formula=frac_hitchhiking_linked_trait_change~condition,
      data=stat_data
   )
  print(
   kt
  if (is.na(kt$p.value)) { next }
  if (kt$p.value > 0.05) { next }
  print(
   pairwise.wilcox.test(
     x=stat_data$frac_hitchhiking_linked_trait_change,
     g=stat_data$condition,
     p.adjust.method="bonferroni",
     exact=FALSE
   )
 )
}
## [1] "PENALTY: O"
##
## Kruskal-Wallis rank sum test
## data: frac_hitchhiking_linked_trait_change by condition
## Kruskal-Wallis chi-squared = 211.29, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: stat_data$frac_hitchhiking_linked_trait_change and stat_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.031
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
##
## Kruskal-Wallis rank sum test
## data: frac_hitchhiking_linked_trait_change by condition
## Kruskal-Wallis chi-squared = 186.88, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
```

```
##
## data: stat_data$frac_hitchhiking_linked_trait_change and stat_data$condition
##
          NON-PLASTIC PLASTIC
## PLASTIC 2.9e-16
## STATIC < 2e-16
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
##
##
   Kruskal-Wallis rank sum test
##
## data: frac_hitchhiking_linked_trait_change by condition
## Kruskal-Wallis chi-squared = 113.72, df = 2, p-value < 2.2e-16
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: stat_data$frac_hitchhiking_linked_trait_change and stat_data$condition
##
          NON-PLASTIC PLASTIC
##
## PLASTIC 3.3e-08
## STATIC < 2e-16
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.3"
##
## Kruskal-Wallis rank sum test
##
## data: frac_hitchhiking_linked_trait_change by condition
## Kruskal-Wallis chi-squared = 34.791, df = 2, p-value = 2.788e-08
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: stat_data$frac_hitchhiking_linked_trait_change and stat_data$condition
##
##
          NON-PLASTIC PLASTIC
## PLASTIC 0.26
## STATIC 2.4e-08
                       0.18
##
## P value adjustment method: bonferroni
denom <- sum(filter(summary_data, condition=="NON-PLASTIC" & POISON_PENALTY==0.1)$domi:
num <- sum(filter(summary_data, condition=="NON-PLASTIC" & POISON_PENALTY==0.1)$dominates
pasteO("NON-PLASTIC: ", num/denom, "(", num, "/", denom, ")")
```

```
## [1] "NON-PLASTIC: 0.498956158663883(956/1916)"
denom <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_num
num <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_num
pasteO("PLASTIC: ", num/denom, " (", num, "/", denom, ")")

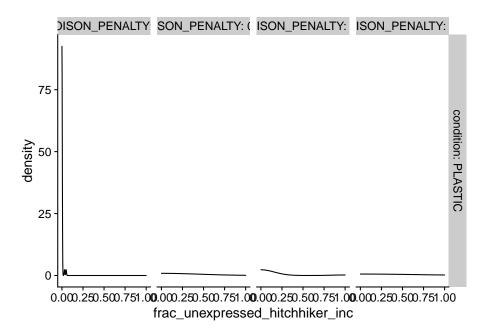
## [1] "PLASTIC: 0 (0/18)"

denom <- sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_lineage_num
num <- sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_lineage_num_num <- sum(filter(summary_data, sondition=="STATIC" & POISON_PENALTY==0.1
```

# 5.7 What fraction of poison execution increases occur in unexpressed phenotype (as cryptic

```
summary_data$frac_unexpressed_hitchhiker_inc <- summary_data$dominant_lineage_num_times_hitchhike
summary_data$frac_expressed_hitchiker_inc <- summary_data$dominant_lineage_num_times_hitchhike_ir

ggplot(filter(summary_data, dominant_lineage_num_times_hitchhike_inst_exec_increases>0 & condition
geom_density() +
facet_grid(
    condition~POISON_PENALTY,
    labeller=label_both,
    scales="free_y"
) +
theme(
    legend.position="none"
```



```
denom <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant
num <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_1
paste0("PLASTIC: ", num/denom, " (", num, "/", denom, ")")</pre>
```

## 5.8 Manuscript figures

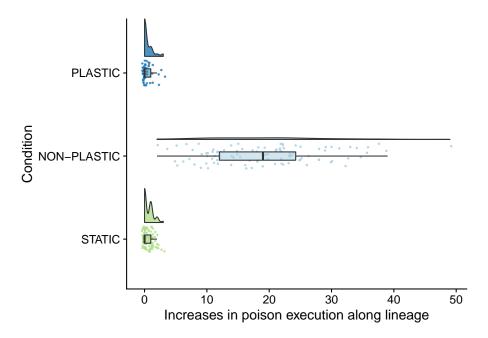
## [1] "PLASTIC: 0.0555555555556 (1/18)"

```
poison_penalty <- 0.1
```

#### 5.8.1 Total poison execution increases along lineage.

```
poison_increases_fig <- ggplot(
    filter(summary_data, POISON_PENALTY==poison_penalty),
    aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases, fill=
) +
    geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
    geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,</pre>
```

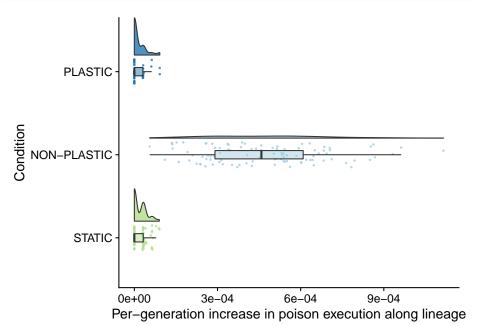
```
alpha = 0.8
 ) +
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 ) +
  scale_y_continuous(
   name="Increases in poison execution along lineage",
  scale_fill_brewer(
   palette="Paired"
 scale_color_brewer(
   palette="Paired"
 ) +
 theme(
   legend.position="none"
 ) +
 coord_flip()
poison_increases_fig
```



# 5.8.2 Per-generation poison execution increases along lineage

```
poison_increases_per_gen_fig <- ggplot(</pre>
    filter(summary_data, POISON_PENALTY==poison_penalty),
    aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases_per_get
  ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
    name="Condition",
```

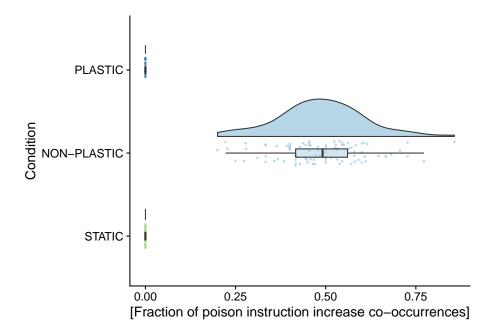
```
limits=condition_order,
   labels=condition_order
) +
scale_y_continuous(
   name="Per-generation increase in poison execution along lineage",
) +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
theme(
   legend.position="none"
) +
coord_flip()
```



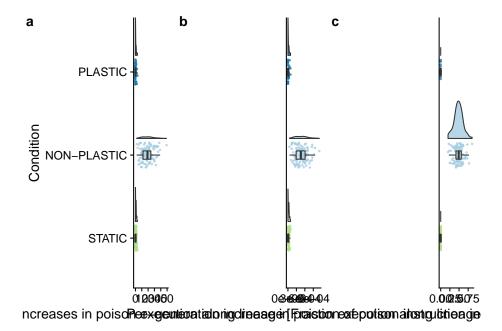
#### 5.8.3 Co-occurrence

```
linked_trait_change_fig <- ggplot(
    filter(summary_data, POISON_PENALTY==poison_penalty & dominant_lineage_num_times_hitchhike_ir
    aes(x=condition, y=frac_hitchhiking_linked_trait_change, fill=condition)</pre>
```

```
) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
    name="Condition",
    limits=condition_order,
   labels=condition_order
  ) +
  scale_y_continuous(
   name="[Fraction of poison instruction increase co-occurrences]",
  scale_fill_brewer(
   palette="Paired"
  ) +
  scale_color_brewer(
    palette="Paired"
  ) +
  theme(
    legend.position="none"
  coord_flip()
linked_trait_change_fig
```



```
grid <- plot_grid(
  poison_increases_fig,
  poison_increases_per_gen_fig + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(
```



# Chapter 6

# Regulation in Avida

#### 6.1 Overview

```
total_updates <- 2000000
replicates <- 100

all_traits <- c("not", "nand", "and", "ornot", "or", "andnot")
traits_set_a <- c("not", "and", "or")
traits_set_b <- c("nand", "ornot", "andnot")

# Relative location of data.
working_directory <- "experiments/2021-02-08-evo-dynamics/analysis/" # << For bookdown
# working_directory <- "./" # << For local analysis</pre>
```

## 6.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
library(RColorBrewer)
library(Hmisc)
library(boot)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd97121f7f9ce9
```

These analyses were conducted/knitted with the following computing environment:

```
print(version)
##
## platform
                  x86_64-pc-linux-gnu
## arch
                  x86 64
## os
                  linux-gnu
## system
                  x86_64, linux-gnu
## status
## major
                  0.4
## minor
## year
                  2021
## month
                  02
## day
                  15
                  80002
## svn rev
## language
                  R
## version.string R version 4.0.4 (2021-02-15)
                 Lost Library Book
## nickname
```

### 6.3 Setup

```
trace_summary_data_loc <- paste0(working_directory, "data/trace_summary.csv")</pre>
trace_summary_data <- read.csv(trace_summary_data_loc, na.strings="NONE")</pre>
trace_summary_data$DISABLE_REACTION_SENSORS <- as.factor(trace_summary_data$DISABLE_RE.
trace_summary_data$chg_env <- trace_summary_data$chg_env == "True"</pre>
trace_summary_data$sensors <- trace_summary_data$DISABLE_REACTION_SENSORS == "0"</pre>
env_label_fun <- function(chg_env) {</pre>
  if (chg_env) {
    return("Fluctuating")
  } else {
    return("Constant")
  }
}
sensors_label_fun <- function(has_sensors) {</pre>
  if (has_sensors) {
    return("Sensors")
  } else {
    return("No sensors")
  }
}
```

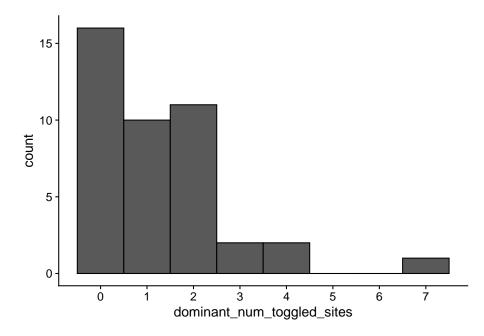
```
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
 } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
 }
}
trace_summary_data$env_label <- mapply(</pre>
  env_label_fun,
  trace_summary_data$chg_env
trace_summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  trace_summary_data$sensors
trace_summary_data$condition <- mapply(</pre>
  condition_label_fun,
  trace_summary_data$sensors,
  trace_summary_data$chg_env
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
```

# 6.4 How many instructions do plastic genomes toggle depending on environmental context?

```
ggplot(trace_summary_data, aes(x=dominant_num_toggled_sites)) +
    geom_histogram(
        binwidth=1,
        color="black"
    ) +
    scale_fill_brewer(
        palette="Paired"
    ) +
    scale_color_brewer(
        palette="Paired"
```

```
) +
scale_x_continuous(
   breaks=seq(0, max(trace_summary_data$dominant_num_toggled_sites)+1)
) +
theme(
  legend.position="none"
) +
ggsave(paste0(working_directory, "plots/", "toggled-sites.png"))
```

## Saving 6.5 x 4.5 in image



# 6.5 What is the distribution of toggled sequence sizes?

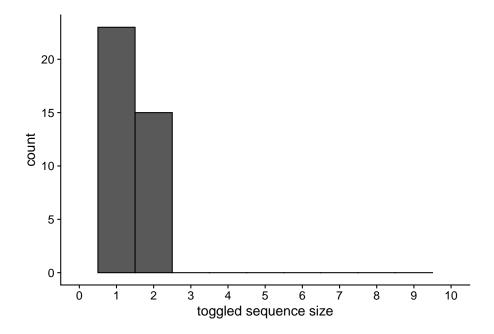
```
chunk_sizes <- data.frame(
    size=integer()
)
for (sizes in trace_summary_data$dominant_toggled_chunk_sizes) {
    if (sizes == "") { next }
        sizes <- unlist(lapply(str_split(sizes, ';'), as.integer))
        chunk_sizes <- rbind(chunk_sizes, data.frame(size=c(sizes)))
}</pre>
```

#### 6.5. WHAT IS THE DISTRUBUTION OF TOGGLED SEQUENCE SIZES?141

```
ggplot(chunk_sizes, aes(x=size)) +
   geom_histogram(
     binwidth=1,
     color="black"
   scale_fill_brewer(
     palette="Paired"
   ) +
   scale_color_brewer(
     palette="Paired"
   scale_x_continuous(
     name="toggled sequence size",
     breaks=seq(0, 10),
     limits=c(0, 10)
   ) +
   theme(
     legend.position="none"
   ggsave(paste0(working_directory, "plots/", "toggled-chunk-sizes.png"))
```

```
## Saving 6.5 \times 4.5 in image
```

```
## Warning: Removed 2 rows containing missing values (geom_bar).
## Warning: Removed 2 rows containing missing values (geom_bar).
```



# Chapter 7

# Evolutionary change (variable length genomes)

#### 7.1 Overview

```
total_updates <- 200000
replicates <- 100

all_traits <- c("not","nand","and","ornot","or","andnot")
traits_set_a <- c("not", "and", "or")
traits_set_b <- c("nand", "ornot", "andnot")

# Relative location of data.
working_directory <- "experiments/2021-01-30-evo-dynamics/analysis/" # << For bookdown
# working_directory <- "./"
# << For local analysis</pre>
```

## 7.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
library(RColorBrewer)
library(Hmisc)
library(boot)
source("https://gist.githubusercontent.com/benmarwick/2a1bb0133ff568cbe28d/raw/fb53bd97121f7f9ce8
```

These analyses were conducted/knitted with the following computing environ-

ment:

```
print(version)
##
                  x86_64-pc-linux-gnu
## platform
## arch
                  x86_64
## os
                  linux-gnu
                  x86_64, linux-gnu
## system
## status
## major
## minor
                  0.4
                  2021
## year
## month
                 02
## day
                 15
## svn rev
                 80002
## language
                 R
## version.string R version 4.0.4 (2021-02-15)
## nickname
                 Lost Library Book
```

## 7.3 Setup

```
summary_data_loc <- paste0(working_directory, "data/aggregate.csv")</pre>
summary_data <- read.csv(summary_data_loc, na.strings="NONE")</pre>
summary_data$DISABLE_REACTION_SENSORS <- as.factor(summary_data$DISABLE_REACTION_SENSO
summary_data$chg_env <- summary_data$chg_env == "True"</pre>
summary_data$dominant_plastic_odd_even <- as.factor(summary_data$dominant_plastic_odd_
summary_data$sensors <- summary_data$DISABLE_REACTION_SENSORS == "0"</pre>
summary_data$is_plastic <- summary_data$dominant_plastic_odd_even == "True"
env_label_fun <- function(chg_env) {</pre>
  if (chg_env) {
   return("Fluctuating")
 } else {
    return("Constant")
 }
sensors_label_fun <- function(has_sensors) {</pre>
  if (has sensors) {
   return("Sensors")
 } else {
    return("No sensors")
```

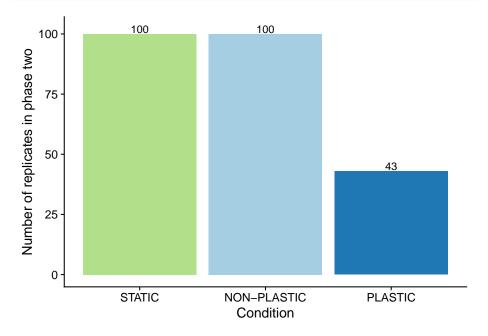
```
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
  } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
 }
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
)
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
)
summary_data$condition <- mapply(</pre>
  condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
condition_order = c(
  "STATIC",
  "NON-PLASTIC",
  "PLASTIC"
)
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
```

### 7.4 Evolution of phenotypic plasticity

For sensor-enabled populations in fluctuating environments, we only transfered populations containing an optimally plastic genotype to phase-two.

```
summary_data_grouped = dplyr::group_by(summary_data, sensors, env_label, condition)
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
```

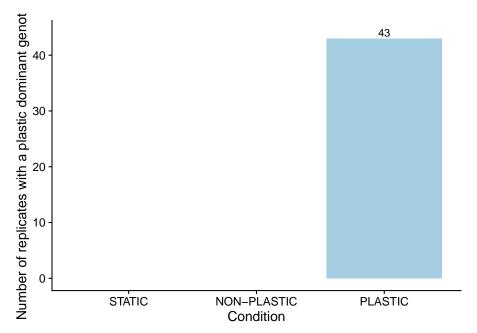
```
## `summarise()` has grouped output by 'sensors', 'env_label'. You can override using 'ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    geom_text(aes(label=n, y=n+2)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    scale_fill_brewer(
        palette="Paired"
) +
    scale_color_brewer(
        palette="Paired"
) +
    ylab("Number of replicates in phase two") +
    theme(
        legend.position="none"
)
```



We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

```
summary_data_grouped = dplyr::group_by(summary_data, condition, is_plastic)
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
```

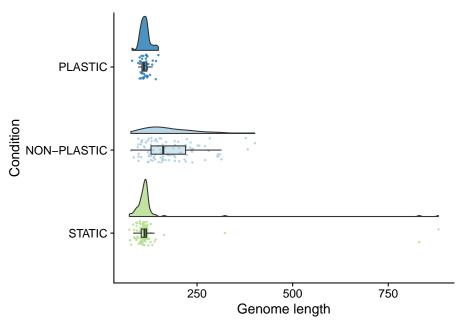
```
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
  geom_col(position=position_dodge(0.9)) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  geom_text(aes(label=n, y=n+1)) +
  ylab("Number of replicates with a plastic dominant genotype") +
  theme(
   legend.position="none"
 )
```



### 7.5 Genome length

Single-instruction insertions and deletions were possible for this experiment, so genome size also evolved.

```
ggplot(summary_data, aes(x=condition, y=dominant_genome_length, fill=condition)) +
 geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
   palette="Paired"
 ) +
  scale_color_brewer(
   palette="Paired"
  coord_flip() +
 ylab("Genome length") +
 theme(
    legend.position="none"
```



```
kruskal.test(
 formula=dominant_genome_length~condition,
  data=summary_data
)
##
   Kruskal-Wallis rank sum test
##
##
## data: dominant_genome_length by condition
## Kruskal-Wallis chi-squared = 82.798, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=summary_data$dominant_genome_length,
  g=summary_data$condition,
 p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$dominant_genome_length and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC 1.8e-10
## STATIC < 2e-16
##
```

```
## P value adjustment method: bonferroni
median(filter(summary_data, condition=="PLASTIC")$phylo_mrca_changes)

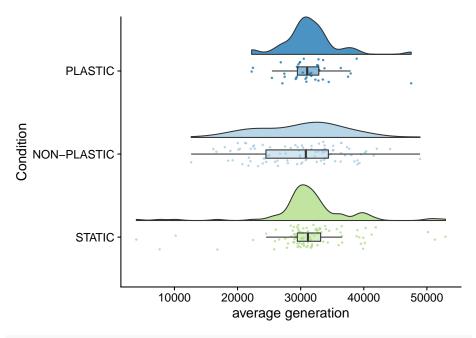
## [1] 45
median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)

## [1] 47
median(filter(summary_data, condition=="NON-PLASTIC")$phylo_mrca_changes)

## [1] 393
```

### 7.6 Average generation

```
ggplot(summary_data, aes(x=condition, y=time_average_generation, fill=condition)) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  scale_fill_brewer(
   palette="Paired"
 scale_color_brewer(
   palette="Paired"
  coord flip() +
 ylab("average generation") +
 theme(
    legend.position="none"
```

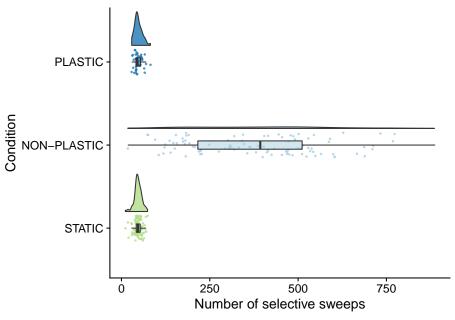


```
median(filter(summary_data, condition=="PLASTIC")$time_average_generation)
## [1] 31028.6
median(filter(summary_data, condition=="STATIC")$time_average_generation)
## [1] 31147.5
median(filter(summary_data, condition=="NON-PLASTIC")$time_average_generation)
## [1] 30817.95
kruskal.test(
  formula=time_average_generation~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
##
## data: time_average_generation by condition
## Kruskal-Wallis chi-squared = 1.3804, df = 2, p-value = 0.5015
```

### 7.7 Coalescence events

The number of times the most recent common ancestor changes gives us the number of selective sweeps that occur during the experiment.

```
ggplot(summary_data, aes(x=condition, y=phylo_mrca_changes, fill=condition)) +
 geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
    palette="Paired"
  ) +
  coord_flip() +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ylab("Number of selective sweeps") +
 theme(
    legend.position="none"
```



```
paste0(
 "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$phylo_mrca_changes)
## [1] "PLASTIC: 45"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)
)
## [1] "STATIC: 47"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$phylo_mrca_changes)
## [1] "NON-PLASTIC: 393"
kruskal.test(
  formula=phylo_mrca_changes~condition,
  data=summary_data
)
##
## Kruskal-Wallis rank sum test
```

```
##
## data: phylo_mrca_changes by condition
## Kruskal-Wallis chi-squared = 168.89, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$phylo_mrca_changes,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary data$phylo mrca changes and summary data$condition
##
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
## P value adjustment method: bonferroni
```

## 7.7.1 Average number of generations between selective sweeps

```
summary data$generations per mrca change <- summary data$time average generation / sum
ggplot(summary_data, aes(x=condition, y=generations_per_mrca_change, fill=condition))
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
    outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
    limits=condition_order
```

## [1] "STATIC: 668.25523255814"

```
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
)
```

```
PLASTIC NON-PLASTIC STATIC 250 500 750 1000 generations_per_mrca_change
```

```
paste0(
   "PLASTIC: ",
   median(filter(summary_data, condition=="PLASTIC")$generations_per_mrca_change)
)

## [1] "PLASTIC: 695.504761904762"

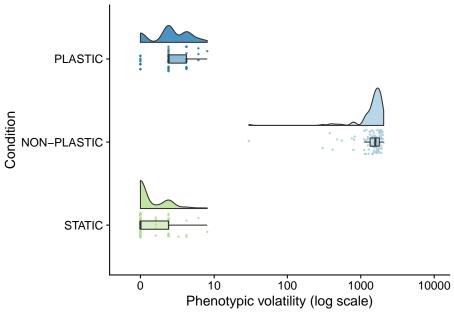
paste0(
   "STATIC: ",
   median(filter(summary_data, condition=="STATIC")$generations_per_mrca_change)
)
```

```
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$generations_per_mrca_change)
## [1] "NON-PLASTIC: 81.9208459944751"
kruskal.test(
  formula=generations_per_mrca_change~condition,
  data=summary_data
##
##
   Kruskal-Wallis rank sum test
## data: generations_per_mrca_change by condition
## Kruskal-Wallis chi-squared = 171.73, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$generations_per_mrca_change,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$generations_per_mrca_change and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
## P value adjustment method: bonferroni
```

# 7.8 Phenotypic volatility along the dominant lineage

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_volatility, fill=condit
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
) +
  geom_point(
    mapping=aes(color=condition),
```

```
position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
 width = .1,
  outlier.shape = NA,
 alpha = 0.5
scale_x_discrete(
 name="Condition",
  limits=condition_order
) +
scale_y_continuous(
 name="Phenotypic volatility (log scale)",
 trans="pseudo_log",
 breaks=c(0, 10, 100, 1000, 10000),
 limits=c(-1,10000)
) +
scale_fill_brewer(
  palette="Paired"
) +
scale_color_brewer(
 palette="Paired"
) +
coord_flip() +
theme(
  legend.position="none"
```



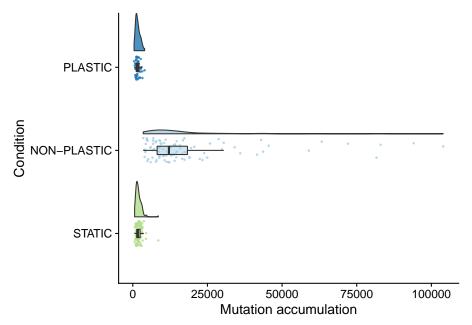
```
paste0(
  "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility)
## [1] "PLASTIC: 2"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility)
## [1] "STATIC: O"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volatil
## [1] "NON-PLASTIC: 1580"
kruskal.test(
  formula=dominant_lineage_trait_volatility~condition,
  data=summary_data
)
##
## Kruskal-Wallis rank sum test
```

```
##
## data: dominant_lineage_trait_volatility by condition
## Kruskal-Wallis chi-squared = 191.98, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$dominant_lineage_trait_volatility,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
## data: summary data$dominant lineage trait volatility and summary data$condition
##
          NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       5.2e-08
## P value adjustment method: bonferroni
```

# 7.9 Mutation accumulation along the dominant lineage

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_total_mut_cnt, fill=condition)) +
  geom flat violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ylab("Mutation accumulation") +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
```

```
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
coord_flip() +
theme(
   legend.position="none"
)
```



```
paste0(
   "PLASTIC: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_total_mut_cnt)
)

## [1] "PLASTIC: 1552"

paste0(
   "STATIC: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_total_mut_cnt)
)

## [1] "STATIC: 1724.5"
```

#### 7.9. MUTATION ACCUMULATION ALONG THE DOMINANT LINEAGE161

```
paste0(
 "NON-PLASTIC: ",
 median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_total_mut_cnt)
## [1] "NON-PLASTIC: 12123"
kruskal.test(
  formula=dominant_lineage_total_mut_cnt~condition,
  data=summary_data
)
##
   Kruskal-Wallis rank sum test
##
## data: dominant_lineage_total_mut_cnt by condition
## Kruskal-Wallis chi-squared = 174.38, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=summary_data$dominant_lineage_total_mut_cnt,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$dominant_lineage_total_mut_cnt and summary_data$condition
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                      0.57
##
## P value adjustment method: bonferroni
```