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Chapter 1

Introduction

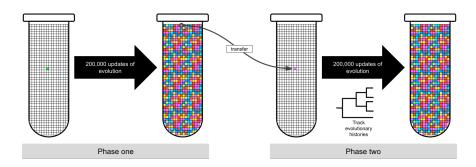


Figure 1.1: Experimental design overview

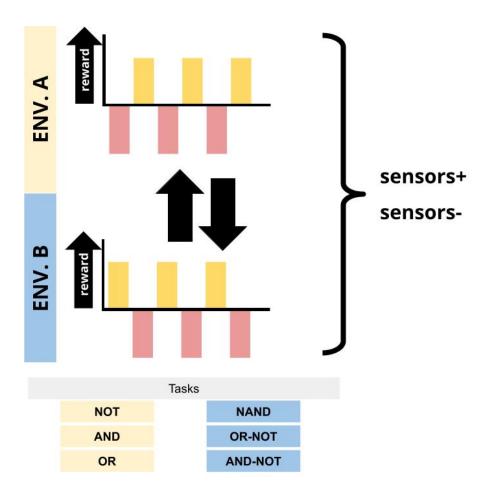


Figure 1.2: Fluctuating environment

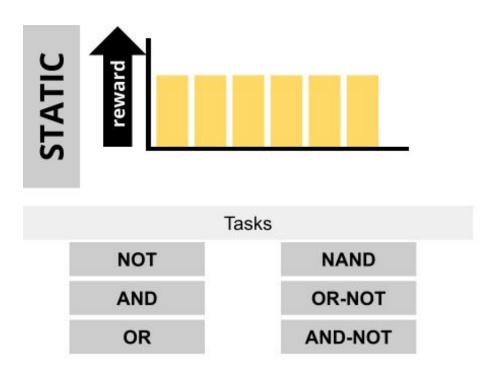


Figure 1.3: Static environment

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
                  0.5
                  2021
## year
## month
                  03
## day
                  31
                  80133
## svn rev
                  R
## language
## version.string R version 4.0.5 (2021-03-31)
## nickname
                  Shake and Throw
```

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
alpha <- 0.05

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(rstatix)
library(ggsignif)
library(scales)
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)
##
                  x86_64-pc-linux-gnu
## platform
## arch
                  x86_64
## os
                  linux-gnu
                  x86_64, linux-gnu
## system
## status
## major
                  0.5
## minor
## year
                  2021
## month
                  03
                  31
## day
## svn rev
                  80133
                  R
## language
## version.string R version 4.0.5 (2021-03-31)
                Shake and Throw
## nickname
```

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) {
```

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```
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"
)
pairwise_comparisons <- list(</pre>
  c("STATIC", "NON-PLASTIC"),
  c("STATIC", "PLASTIC"),
  c("PLASTIC", "NON-PLASTIC")
p_label <- function(p_value) {</pre>
  threshold = 0.0001
  if (p_value < threshold) {</pre>
```

```
return(paste0("p < ", threshold))</pre>
  } else {
    return(paste0("p = ", p_value))
  }
}
# *really* inefficient way to identify outliers
is_outlier <- function(value, cond, data, column) {</pre>
  cond_data <- filter(data, condition==cond)</pre>
  q1 <- summary(cond_data[,column])[["1st Qu."]]
  q3 <- summary(cond_data[,column])[["3rd Qu."]]
  H <- 1.5 * IQR(cond data[,column])</pre>
  return( (value < (q1-H)) || (value > (q3+H)) )
###### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
# Palette
cb_palette <- "Paired"
# 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]))
```

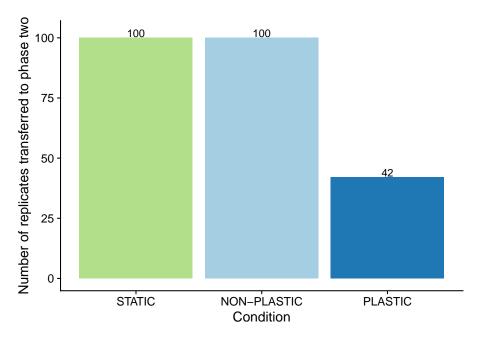
3.4 The evolution of phenotypic plasticity

For sensor-enabled populations in fluctuating environments, we only transfered 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=cb_palette
) +
```

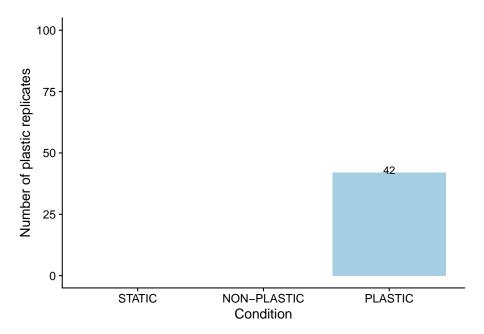
```
scale_color_brewer(
   palette=cb_palette
) +
ylab("Number of replicates transferred to phase two") +
theme(
  legend.position="none"
)
```



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=cb_palette
) +
scale_color_brewer(
```

```
palette=cb_palette
) +
geom_text(aes(label=n, y=n+1)) +
ylab("Number of plastic replicates") +
ylim(0, 100) +
theme(
  legend.position="none"
)
```

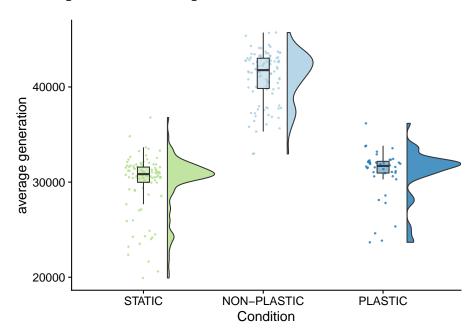


3.5 Average generation

```
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=cb_palette
scale_color_brewer(
  palette=cb_palette
) +
# coord_flip() +
ylab("average generation") +
theme(
  legend.position="none"
ggsave(paste0(working_directory, "plots/", "average-generation.png"))
```

Saving 6.5×4.5 in image



```
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
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$time_average_generation)
  ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$time_average_generation)
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$time_average_generation)
  )
)
## [1] "PLASTIC median: 31697.65; STATIC median: 30839.75; NON-PLASTIC median: 41768.6
print("Wilcox rank sum test statistics:")
```

[1] "Wilcox rank sum test statistics:"

```
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(</pre>
    formula=time_average_generation~condition,
    data=pair_data,
    exact=FALSE,
   paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=9982"
## [1] "STATIC<-->PLASTIC: W=2818"
## [1] "PLASTIC<-->NON-PLASTIC: W=4186"
summary_data %>%
  group_by(condition) %>%
  summarise(mean=mean(time_average_generation),sd=sd(time_average_generation))
## # A tibble: 3 x 3
## condition mean
                <dbl> <dbl>
   <chr>
## 1 NON-PLASTIC 41090. 2702.
## 2 PLASTIC 31016. 2615.
## 3 STATIC
                 30002. 3011.
```

3.6 Coalescence event count

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

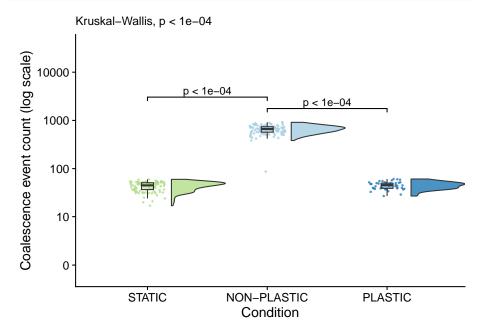
```
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(phylo_mrca_changes ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition",step.increase=1)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in general stat.test$manual_position <- log10(stat.test$y.position) * c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)

summary_data$is_outlier <- mapply(
  is_outlier,
  summary_data$phylo_mrca_changes,
  summary_data$condition,</pre>
```

```
MoreArgs=list(data=summary_data, column="phylo_mrca_changes")
coalescence_events_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=phylo_mrca_changes,fill=condition)
  geom_flat_violin(
   data=filter(summary_data,is_outlier==FALSE),
    scale="width",
   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,
   breaks=condition order
  ) +
  scale_y_continuous(
   name="Coalescence event count (log scale)",
   trans=pseudo_log_trans(sigma = 1, base = 10),
   breaks=c(0, 10, 100, 1000, 10000),
   limits=c(-1, 35000)
 ) +
  scale_fill_brewer(
   palette=cb_palette
  scale_color_brewer(
   palette=cb_palette
  ) +
 labs(
    subtitle=paste0(
      "Kruskal-Wallis, ",
```

```
p_label(signif(kruskal.test(formula=phylo_mrca_changes~condition, data=summary_data)$p.valu
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
# coord_flip() +
theme(
  legend.position="none"
) +
ggsave(
  pasteO(working_directory, "plots/", "selective-sweeps.pdf"),
  width=5,
  height=5
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
coalescence_events_fig



```
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
paste(
 sep="; ",
 paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$phylo_mrca_changes)
 ),
 paste0(
   "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)
 ),
 paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$phylo_mrca_changes)
## [1] "PLASTIC median: 45.5; STATIC median: 45; NON-PLASTIC median: 663.5"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
```

```
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)
  pair_data$condition <- as.factor(pair_data$condition)
  wt <- wilcox.test(
    formula=phylo_mrca_changes~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
)
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
}

## [1] "STATIC<-->NON-PLASTIC: W=10000"
## [1] "STATIC<-->PLASTIC: W=2215"
## [1] "PLASTIC<-->NON-PLASTIC: W=4200"
```

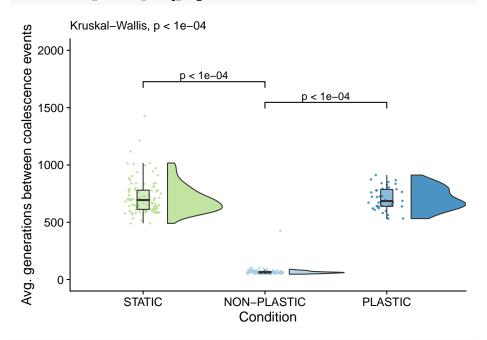
3.6.1 Average number of generations between coalescence events

```
# Compute frequency of coalescence events
summary_data$generations_per_mrca_change <- summary_data$time_average_generation / summary_data$f
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(generations_per_mrca_change ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition")
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- stat.test$y.position</pre>
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
summary_data$is_outlier <- mapply(</pre>
  is_outlier,
  summary_data$generations_per_mrca_change,
  summary_data$condition,
  MoreArgs=list(data=summary_data, column="generations_per_mrca_change")
)
coalescence_events_freq_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=generations_per_mrca_change, fill=condition)
 ) +
  geom_flat_violin(
    data=filter(summary_data,is_outlier==FALSE),
```

```
scale="width",
  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="Avg. generations between coalescence events",
 limits=c(0, 2000),
 breaks=seq(0, 2000, 500)
) +
scale fill brewer(
 palette=cb_palette
scale_color_brewer(
  palette=cb_palette
) +
# coord_flip() +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=generations_per_mrca_change~condition, data=
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y position=manual position),
 manual=TRUE,
 inherit.aes=FALSE
) +
theme(
```

```
legend.position="none"
) +
ggsave(
  paste0(working_directory, "plots/", "generations-between-selective-sweeps.png"),
  width=5,
  height=5
)
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
coalescence_events_freq_fig



```
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,</pre>
```

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
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ".
    median(filter(summary_data, condition=="PLASTIC")$generations_per_mrca_change)
  ),
  paste0(
    "STATIC median: ",
    median(filter(summary_data, condition=="STATIC")$generations_per_mrca_change)
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$generations_per_mrca_change)
  )
)
## [1] "PLASTIC median: 685.001780758557; STATIC median: 693.676265008576; NON-PLASTIC
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(</pre>
    formula=generations_per_mrca_change~condition,
    data=pair data,
    exact=FALSE,
    paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=0"
```

```
## [1] "STATIC<-->PLASTIC: W=2151"
## [1] "PLASTIC<-->NON-PLASTIC: W=0"
```

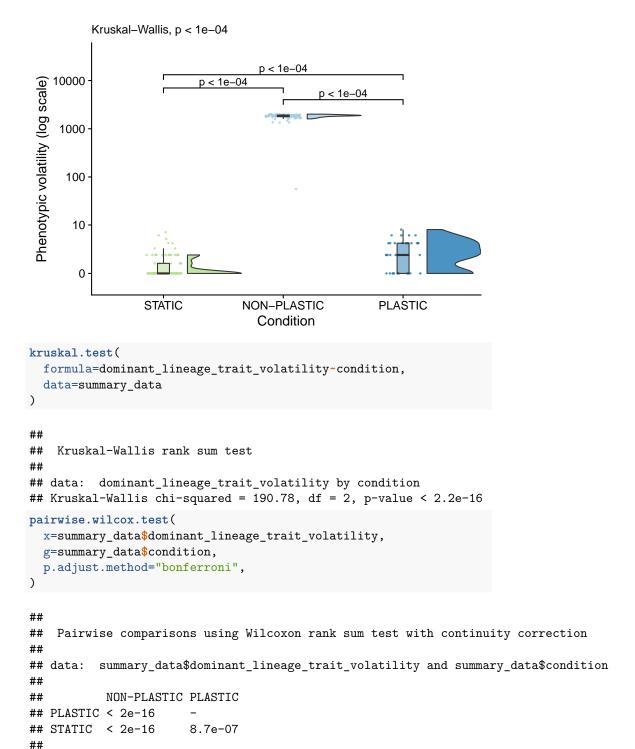
3.7 Phenotypic volatility along the dominant lineage

```
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(dominant_lineage_trait_volatility ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition", step.increase=1)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- log10(stat.test$y.position) * c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
summary_data$is_outlier <- mapply(</pre>
  is outlier,
  summary_data$dominant_lineage_trait_volatility,
  summary_data$condition,
 MoreArgs=list(data=summary_data, column="dominant_lineage_trait_volatility")
phenotypic_volatility_fig <- ggplot(</pre>
    summary data,
    aes(x=condition, y=dominant_lineage_trait_volatility, fill=condition)
  geom_flat_violin(
   data=filter(summary_data,is_outlier==FALSE),
    scale="width",
   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_trans(sigma = 1, base = 10),
  breaks=c(0, 10, 100, 1000, 10000),
 limits=c(-1, 35000)
scale fill brewer(
  palette=cb_palette
scale_color_brewer(
 palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_trait_volatility~condition,
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj<=alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
 manual=TRUE,
 inherit.aes=FALSE
) +
# coord_flip() +
theme(
  legend.position="none"
ggsave(
  pasteO(working_directory, "plots/", "phenotypic-volatility.pdf"),
  width=5,
  height=5
)
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
phenotypic_volatility_fig

3.7. PHENOTYPIC VOLATILITY ALONG THE DOMINANT LINEAGE33



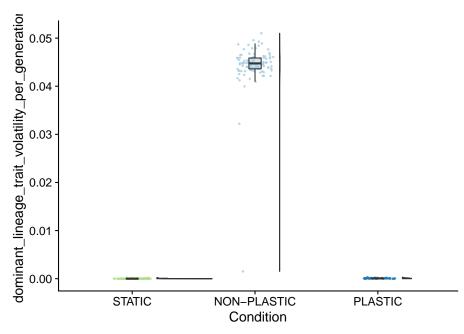
```
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
    median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatilit
 ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility
 ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volat
  )
## [1] "PLASTIC median: 2; STATIC median: 0; NON-PLASTIC median: 1868"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
   formula=dominant_lineage_trait_volatility~condition,
   data=pair data,
    exact=FALSE,
   paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
}
## [1] "STATIC<-->NON-PLASTIC: W=10000"
## [1] "STATIC<-->PLASTIC: W=3116.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=4200"
```

3.7.1 Phenotypic volatility normalized by generations elapsed

```
summary_data$dominant_lineage_trait_volatility_per_generation <- summary_data$dominant
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_volatility_per_generation
geom_flat_violin(</pre>
```

```
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=cb_palette
scale_color_brewer(
  palette=cb_palette
) +
# coord_flip() +
theme(
  legend.position="none"
```

##



```
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",
)</pre>
```

```
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
    median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility_per_gener
  ),
  paste0(
    "STATIC median: ",
    median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility_per_generate
 ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volatility_per_g
)
## [1] "PLASTIC median: 6.33339279717772e-05; STATIC median: 0; NON-PLASTIC median: 0.04474401456
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
    formula=dominant_lineage_trait_volatility_per_generation~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=10000"
## [1] "STATIC<-->PLASTIC: W=3061.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=4200"
```

3.8 Phenotypic fidelity

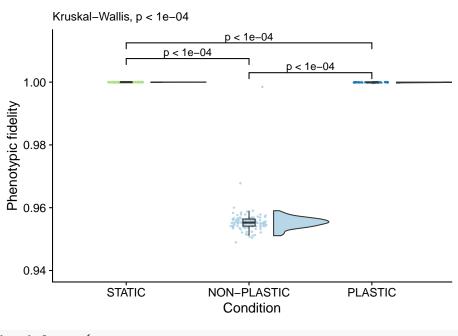
Frequency that an offspring's genotype is identical to a parent genotype (along the dominant lineage).

```
summary_data$dominant_lineage_trait_fidelity <- (summary_data$dominant_generation_born - summary_
# Compute manual labels for geom_signif</pre>
```

```
stat.test <- summary_data %>%
  wilcox_test(dominant_lineage_trait_fidelity ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
 add_xy_position(x="condition",step.increase=1.5)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test$manual_position <- stat.test$y.position * c(1.0,1.0,1.0005)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
summary_data$is_outlier <- mapply(</pre>
 is outlier,
 summary_data$dominant_lineage_trait_fidelity,
 summary data$condition,
 MoreArgs=list(data=summary_data, column="dominant_lineage_trait_fidelity")
phenotypic_fidelity_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_trait_fidelity, fill=condition)
 geom_flat_violin(
    data=filter(summary_data,is_outlier==FALSE),
    scale="width",
    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, 1.013),
  breaks=c(0.94, 0.96, 0.98, 1.0) #seq(0.94, 1.0, 0.01)
scale_fill_brewer(
  palette=cb_palette
scale_color_brewer(
  palette=cb_palette
# coord_flip() +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_trait_fidelity~condition, data=summary
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
ggsave(
  pasteO(working_directory, "plots/", "phenotypic-fidelity.pdf"),
  width=5,
  height=5
)
```

```
## Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
phenotypic_fidelity_fig
```



```
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",
)</pre>
```

adjust_pvalue(method = "bonferroni") %>%

add_significance() %>%

```
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_fidelity)
  ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_fidelity)
  ),
  paste0(
    "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_fidelity)
)
## [1] "PLASTIC median: 0.999936666072028; STATIC median: 1; NON-PLASTIC median: 0.95525598543618
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
 wt <- wilcox.test(
   formula=dominant_lineage_trait_fidelity~condition,
   data=pair_data,
   exact=FALSE,
   paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=0"
## [1] "STATIC<-->PLASTIC: W=1138.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=0"
3.9
       Mutation count
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
 wilcox_test(dominant_lineage_total_mut_cnt ~ condition) %>%
```

```
add_xy_position(x="condition",step.increase=1)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test\$manual_position <- log10(stat.test\$y.position) * c(1.0,1.0,1.03) # c(1.0,1.
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
summary_data$is_outlier <- mapply(</pre>
  is_outlier,
  summary_data$dominant_lineage_total_mut_cnt,
  summary_data$condition,
 MoreArgs=list(data=summary_data, column="dominant_lineage_total_mut_cnt")
mutation_count_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_total_mut_cnt, fill=condition)
  geom_flat_violin(
    data=filter(summary_data, !is_outlier),
    scale="width",
    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="Mutation count (log scale)",
    trans=pseudo_log_trans(sigma = 1, base = 10),
    breaks=c(0, 10, 100, 1000, 10000),
    limits=c(-1, 35000)
  ) +
  scale_fill_brewer(
```

```
palette=cb_palette
scale_color_brewer(
 palette=cb_palette
) +
# coord_flip() +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
   p_label(signif(kruskal.test(formula=dominant_lineage_total_mut_cnt~condition, data=summary)
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
ggsave(
 pasteO(working_directory, "plots/", "mutation-accumulation.pdf"),
  height=4
```

^{##} Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
mutation_count_fig

##

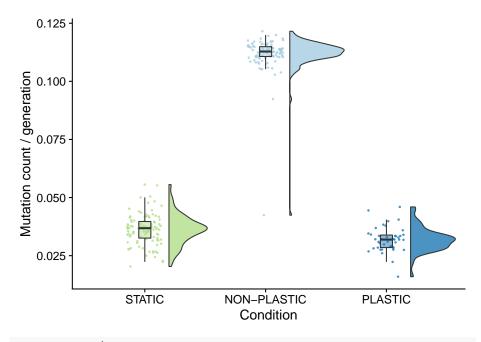
```
Kruskal-Wallis, p < 1e-04
                                  p = 0.001944
                          p < 1e-04
   10000
 Mutation count (log scale)
    1000
     100
      10
       0
                                 NON-PLASTIC
                 STATIC
                                                      PLASTIC
                                   Condition
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 = 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
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
    median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_total_mut_cnt)
  ),
  paste0(
    "STATIC median: ",
    median(filter(summary_data, condition=="STATIC")$dominant_lineage_total_mut_cnt)
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_total_mut_cnt)
  )
)
## [1] "PLASTIC median: 998.5; STATIC median: 1100; NON-PLASTIC median: 4657.5"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
 wt <- wilcox.test(</pre>
    formula=dominant_lineage_total_mut_cnt~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=10000"
## [1] "STATIC<-->PLASTIC: W=1336.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=4200"
```

3.9.1 Mutation count normalized by generations elapsed

```
summary_data$mutations_per_generation <- summary_data$dominant_lineage_total_mut_cnt / summary_data
ggplot(summary_data, aes(x=condition, y=mutations_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("Mutation count / generation") +
 scale_fill_brewer(
   palette=cb_palette
 ) +
 scale_color_brewer(
   palette=cb_palette
 ) +
 # coord_flip() +
 theme(
   legend.position="none"
```



```
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
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
    median(filter(summary_data, condition=="PLASTIC")$mutations_per_generation)
  ),
  paste0(
    "STATIC median: ",
    median(filter(summary_data, condition=="STATIC")$mutations_per_generation)
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$mutations_per_generation)
## [1] "PLASTIC median: 0.0319267181456982; STATIC median: 0.0368157192941933; NON-PLA
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
    formula=mutations_per_generation~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=9987"
## [1] "STATIC<-->PLASTIC: W=1206"
## [1] "PLASTIC<-->NON-PLASTIC: W=4198"
```

3.10 Genotypic fidelity

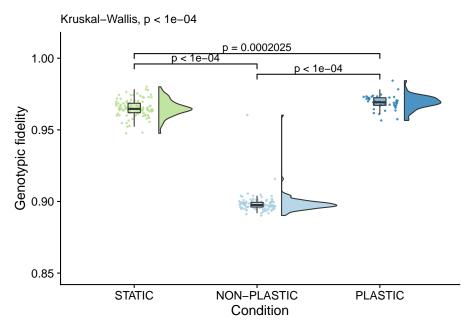
The frequency that an offspring's genotype is the same as a parent's genotype.

```
summary_data$dominant_lineage_genotypic_fidelity <- (summary_data$dominant_generation_'
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
```

```
wilcox_test(dominant_lineage_genotypic_fidelity ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition",step.increase=0.2)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- stat.test$y.position * c(1.0,1.0,1.0)</pre>
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
genotypic_fidelity_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=dominant_lineage_genotypic_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="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=cb_palette
  scale_color_brewer(
    palette=cb_palette
  ) +
  # coord_flip() +
  labs(
```

```
subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_genotypic_fidelity~condition)
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
ggsave(
  pasteO(working_directory, "plots/", "genotypic-fidelity.pdf"),
  width=5,
  height=4
)
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
genotypic_fidelity_fig



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
                       2e-04
## STATIC <2e-16
## P value adjustment method: bonferroni
paste(
 sep="; ",
  paste0(
   "PLASTIC median: ",
   median(filter(summary data, condition=="PLASTIC")$dominant lineage genotypic fidelity)
 ),
  paste0(
   "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_genotypic_fidelity)
  ),
  paste0(
    "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_genotypic_fidelity)
  )
)
## [1] "PLASTIC median: 0.969286906891951; STATIC median: 0.964620594632577; NON-PLASTIC median:
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
```

```
for (pair in pairwise_comparisons) {
   pair_data <- filter(summary_data, condition %in% pair)
   pair_data$condition <- as.factor(pair_data$condition)
   wt <- wilcox.test(
      formula=dominant_lineage_genotypic_fidelity~condition,
      data=pair_data,
      exact=FALSE,
      paired=FALSE
)
   print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
}

## [1] "STATIC<-->NON-PLASTIC: W=18"
## [1] "STATIC<-->PLASTIC: W=2992"
## [1] "PLASTIC<-->NON-PLASTIC: W=2"
```

3.11 Characterizing variation along dominant lineages

3.11.1 Mutational instability

```
summary_data$frac_phenotype_changing_mut_steps <- summary_data$dominant_lineage_num_mu
summary_data$frac_phenotype_stable_mut_steps <- 1 - summary_data$frac_phenotype_changi:
# Compute manual labels for geom_signif
stat.test <- summary data %>%
 wilcox_test(frac_phenotype_changing_mut_steps ~ condition) %>%
 adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
  add_xy_position(x="condition",step.increase=0.2)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test\$manual_position <- stat.test\$y.position #* c(1.0,1.0,1.0)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
ggplot(summary_data, aes(x=condition, y=frac_phenotype_changing_mut_steps, 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
 ylab("Mutational instability") +
 scale fill brewer(
   palette=cb_palette
 scale_color_brewer(
   palette=cb_palette
 # coord_flip() +
 labs(
   subtitle=paste0(
     "Kruskal-Wallis, ",
     p_label(signif(kruskal.test(formula=frac_phenotype_changing_mut_steps~condition, data=summater)
   )
 ) +
 ggsignif::geom_signif(
   data=filter(stat.test, p.adj <= alpha),</pre>
   aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
   manual=TRUE,
   inherit.aes=FALSE
 ) +
 theme(
   legend.position="none"
 ggsave(paste0(working_directory, "plots/", "frac_phenotype_changing_mutational_steps.png"))
```

```
## Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
```

```
## Saving 6.5 x 4.5 in image
```

##

```
Kruskal–Wallis, p < 1e–04

0.8

p < 1e–04

p < 1e–04

0.0-

STATIC

NON–PLASTIC

Condition

NON–PLASTIC

Condition
```

```
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
##
##
          summary_data$frac_phenotype_changing_mut_steps and summary_data$condition
##
           NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       2.3e-07
```

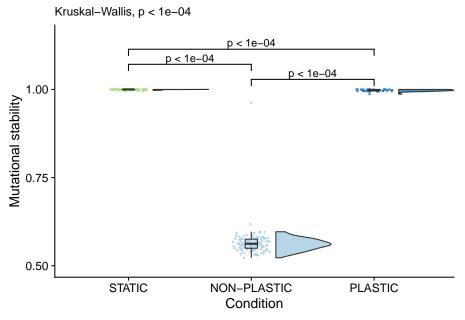
add_xy_position(x="condition",step.increase=0.75)

```
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$frac_phenotype_changing_mut_steps)
  ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$frac_phenotype_changing_mut_steps)
  ),
  paste0(
    "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$frac_phenotype_changing_mut_steps)
  )
)
## [1] "PLASTIC median: 0.00224941742616098; STATIC median: 0; NON-PLASTIC median: 0.437583018324
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
 wt <- wilcox.test(</pre>
    formula=frac_phenotype_changing_mut_steps~condition,
   data=pair_data,
   exact=FALSE,
   paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=10000"
## [1] "STATIC<-->PLASTIC: W=3172"
## [1] "PLASTIC<-->NON-PLASTIC: W=4200"
3.11.2
       Mutational stability
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(frac_phenotype_stable_mut_steps ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
```

```
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test$manual_position <- stat.test$y.position #* c(1.0, 1.0, 1.0)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
summary_data$is_outlier <- mapply(</pre>
  is_outlier,
  summary_data$dominant_lineage_trait_volatility,
  summary_data$condition,
  MoreArgs=list(data=summary_data, column="dominant_lineage_trait_volatility")
mutational_stability_fig <- ggplot(</pre>
    summary_data,
    aes(x=condition, y=frac_phenotype_stable_mut_steps, fill=condition)
  ) +
  geom_flat_violin(
    data=filter(summary_data,is_outlier==FALSE),
    scale="width",
    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="Mutational stability",
    limits=c(0.5, 1.15),
    breaks=c(0.5, 0.75, 1.0)
  scale_fill_brewer(
    palette=cb_palette
  scale_color_brewer(
```

```
palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=frac_phenotype_stable_mut_steps~condition, data=summary
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
mutational_stability_fig



```
kruskal.test(
  formula=frac_phenotype_stable_mut_steps~condition,
  data=summary_data
)
```

```
##
   Kruskal-Wallis rank sum test
##
##
## data: frac_phenotype_stable_mut_steps by condition
## Kruskal-Wallis chi-squared = 191.23, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$frac_phenotype_stable_mut_steps,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$frac_phenotype_stable_mut_steps and summary_data$condition
##
           NON-PLASTIC PLASTIC
##
## PLASTIC < 2e-16
## STATIC < 2e-16
                       2.3e-07
##
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$frac_phenotype_stable_mut_steps)
  ),
  paste0(
    "STATIC median: ",
   median(filter(summary data, condition=="STATIC")$frac phenotype stable mut steps)
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$frac_phenotype_stable_mut_st
  )
)
## [1] "PLASTIC median: 0.997750582573839; STATIC median: 1; NON-PLASTIC median: 0.562
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
```

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```
wt <- wilcox.test(
   formula=frac_phenotype_stable_mut_steps~condition,
   data=pair_data,
   exact=FALSE,
   paired=FALSE
)
print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
}
```

```
## [1] "STATIC<-->NON-PLASTIC: W=0"
## [1] "STATIC<-->PLASTIC: W=1028"
## [1] "PLASTIC<-->NON-PLASTIC: W=0"
```

3.11.3 For PLASTIC populations, what fraction of

```
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).

```
15
  10
count
    5
    0
                               0.4
                                     0.5
        0.0
             0.1
                   0.2
                         0.3
                                           0.6
                                                 0.7
                                                       8.0
                                                             0.9
                                                                   1.0
                          frac_unexpressed_mut_steps
```

```
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 -0.0001867816 0.04000895
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")

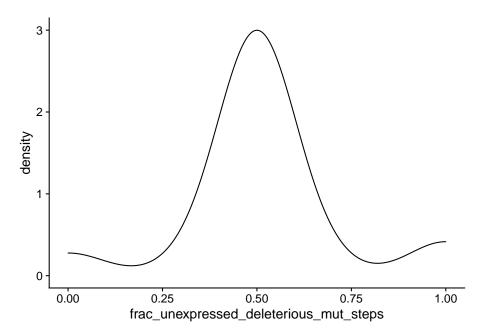
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3.11.4 For PLASTIC populations, what fraction of mutations that affect the unexpressed phenotype are deleterious versus beneficial?

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_steps)

3.11.4.1 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>

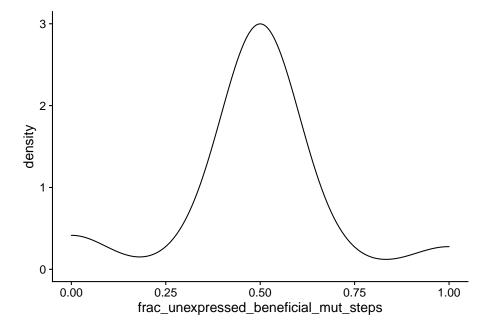
```
##
## ORDINARY NONPARAMETRIC BOOTSTRAP
##
##
## Call:
## boot(data = filter(summary_data, condition == "PLASTIC" & dominant_lineage_num_mut_
##
       0)$frac_unexpressed_deleterious_mut_steps, statistic = samplemean,
       R = 10000)
##
##
##
## Bootstrap Statistics :
        original
                        bias
                                std. error
## t1* 0.5172414 -0.0002450575 0.03949521
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 :
```

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

3.11.4.2 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:
```

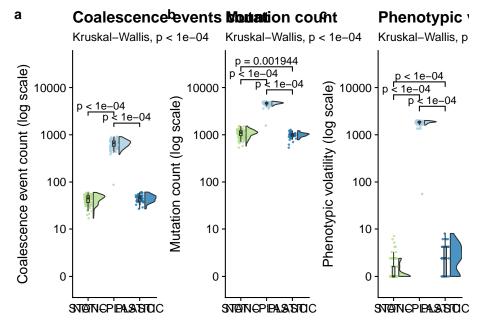
```
## boot(data = filter(summary_data, condition == "PLASTIC" & dominant_lineage_num_mut_:
       0)$frac_unexpressed_beneficial_mut_steps, statistic = samplemean,
       R = 10000)
##
##
##
## Bootstrap Statistics :
        original bias
                               std. error
## t1* 0.4827586 -0.0002364368 0.03949825
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 :
            Percentile
## Level
## 95% ( 0.4034, 0.5597 )
## Calculations and Intervals on Original Scale
```

3.12 Manuscript figures

Figures styled for the paper.

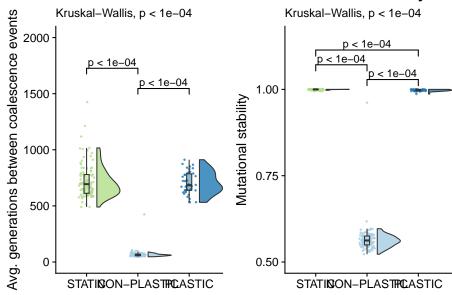
```
magnitude_grid <- plot_grid(</pre>
  coalescence_events_fig +
    theme(
      legend.position="none",
      axis.title.x=element blank()
    ggtitle("Coalescence events count"),
 mutation_count_fig +
    theme(
      legend.position="none",
      axis.title.x=element_blank()
    ggtitle("Mutation count"),
 phenotypic_volatility_fig +
      legend.position="none",
      axis.title.x=element blank()
    ) +
    ggtitle("Phenotypic volatility"),
 nrow=1,
```

```
ncol=3,
align="v",
labels="auto"
)
magnitude_grid
```



```
pace_grid <- plot_grid(</pre>
  coalescence_events_freq_fig +
    theme(
      legend.position="none",
      axis.title.x=element_blank()
    ggtitle("Generations between coalescence events"),
  mutational_stability_fig +
      legend.position="none",
      axis.title.x=element_blank()
    ggtitle("Mutational stability"),
  nrow=1,
 ncol=2,
  align="v",
 labels="auto"
)
pace_grid
```





```
save_plot(
  paste0(working_directory, "plots/", "evolutionary-change-magnitude-panel.pdf"),
 magnitude_grid,
 base_height=6,
  base_asp=3/1
save_plot(
 paste0(working_directory, "plots/", "evolutionary-change-pace-panel.pdf"),
 pace_grid,
 base_height=6,
  base_asp=2/1
# save_plot(
    pasteO(working_directory, "plots/", "evolutionary-change-full-panel.pdf"),
    grid,
    base_height=12,
#
    base_asp=3/2
# )
```

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
alpha <- 0.05
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(
  "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_3bn","logic_3bm",
  "logic_3bn","logic_3bp","logic_3bs",
  "logic_3bt","logic_3bs","logic_3bs",
  "logic_3bt","logic_3bv","logic_3bv",
  "logic_3bw","logic_3bw","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(rstatix)
library(ggsignif)
library(scales)
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
## major
                 4
                 0.5
## minor
## year
                 2021
```

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```
## month 03
## day 31
## svn rev 80133
## language R
## version.string R version 4.0.5 (2021-03-31)
## nickname Shake and Throw
```

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)
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$chg_env
condition_order = c(
  "STATIC",
  "NON-PLASTIC",
  "PLASTIC"
pairwise_comparisons <- list(</pre>
  c("STATIC", "NON-PLASTIC"),
  c("STATIC", "PLASTIC"),
  c("PLASTIC", "NON-PLASTIC")
)
p_label <- function(p_value) {</pre>
  threshold = 0.0001
  if (p_value < threshold) {</pre>
    return(paste0("p < ", threshold))</pre>
  } else {
    return(paste0("p = ", p_value))
  }
}
##### time series #####
lineage_time_series_data_loc <- pasteO(working_directory, "data/lineage_series.csv")</pre>
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_data
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</pre>
lineage_time_series_data$extra_task_value <- as.factor(lineage_time_series_data$extra_
```

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

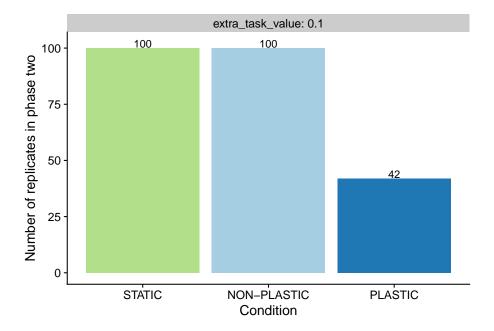
4.4 The evolution of phenotypic plasticity

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_vasummary_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=cb_palette
) +
```

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

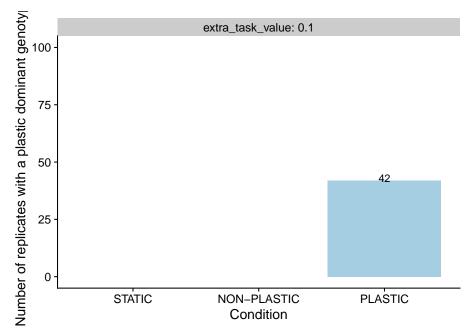


We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

palette=cb_palette

```
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=condition_geom_col(position=position_dodge(0.9)) +
scale_x_discrete(
    name="Condition",
    limits=condition_order
) +
scale_fill_brewer(
    palette=cb_palette
) +
scale_color_brewer(
```

```
) +
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 Final novel task count (dominant genotype)

How many novel tasks do final dominant genotypes perform?

```
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(dominant_extra_tasks ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition") # ,step.increase=1
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in grant stat.test$manual_position <- stat.test$y.position #* c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)
final_novel_task_count_fig <- ggplot(</pre>
```

```
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,
 labels=condition_order
scale y continuous(
 name="Final novel task count"
scale_fill_brewer(
 palette=cb_palette
) +
scale_color_brewer(
 palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_extra_tasks~condition, data=summary
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y position=manual position),
 manual=TRUE,
 inherit.aes=FALSE
) +
# coord_flip()
```

```
theme(
  legend.position="none"
)
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
final_novel_task_count_fig

```
Kruskal–Wallis, p < 1e–04

p < 1e–04

p < 1e–04

p < 1e–04

STATIC NON–PLASTIC PLASTIC Condition
```

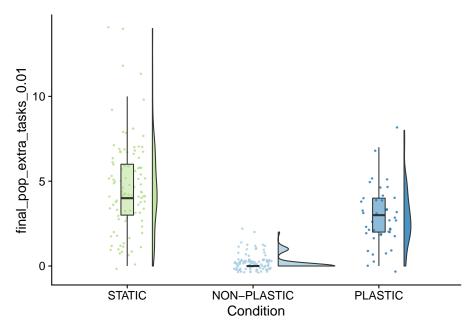
```
kruskal.test(
  formula=dominant_extra_tasks~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
##
## data: dominant_extra_tasks by condition
## Kruskal-Wallis chi-squared = 177.17, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$dominant_extra_tasks,
  g=summary_data$condition,
 p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
```

```
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
##
## data: summary_data$dominant_extra_tasks and summary_data$condition
##
          NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.9
## P value adjustment method: bonferroni
paste(
 sep="; ",
 paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_extra_tasks)
 ),
 paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_extra_tasks)
 ),
 paste0(
    "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$dominant_extra_tasks)
  )
)
## [1] "PLASTIC median: 3; STATIC median: 3; NON-PLASTIC median: 0"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
 wt <- wilcox.test(
   formula=dominant_extra_tasks~condition,
   data=pair_data,
   exact=FALSE,
    paired=FALSE
 print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=184"
## [1] "STATIC<-->PLASTIC: W=1871"
## [1] "PLASTIC<-->NON-PLASTIC: W=64"
```

4.6 Novel task count (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=cb_palette
  scale_color_brewer(
   palette=cb_palette
  ) +
  # coord_flip() +
  theme(
   legend.position="none"
```



```
kruskal.test(
  formula=final_pop_extra_tasks_0.01~condition,
  data=summary_data
)
##
##
   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=summary_data$final_pop_extra_tasks_0.01,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$final_pop_extra_tasks_0.01 and summary_data$condition
##
```

NON-PLASTIC PLASTIC

##

PLASTIC < 2e-16

```
## STATIC < 2e-16
                       0.00016
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$final_pop_extra_tasks_0.01)
  ),
  paste0(
   "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$final_pop_extra_tasks_0.01)
 ),
  paste0(
   "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$final_pop_extra_tasks_0.01)
  )
)
## [1] "PLASTIC median: 3; STATIC median: 4; NON-PLASTIC median: 0"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
   formula=final_pop_extra_tasks_0.01~condition,
   data=pair data,
   exact=FALSE,
   paired=FALSE
  print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=227.5"
## [1] "STATIC<-->PLASTIC: W=1203"
## [1] "PLASTIC<-->NON-PLASTIC: W=225.5"
```

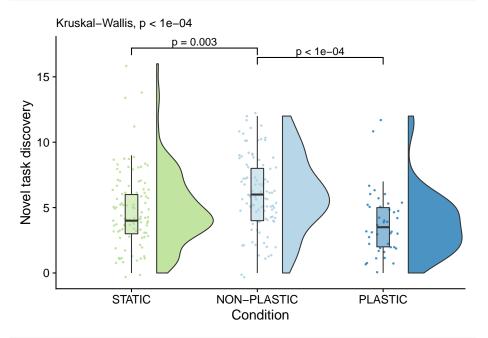
4.7 Novel task discovery (lineage)

```
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
wilcox_test(dominant_lineage_extra_traits_discovered ~ condition) %>%
```

```
adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
  add_xy_position(x="condition") # ,step.increase=1
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test$manual_position <- stat.test$y.position #* c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
lineage_novel_task_discovery_fig <- ggplot(</pre>
    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,
   labels=condition_order
 ) +
 scale_y_continuous(
   name="Novel task discovery"
  scale_fill_brewer(
    palette=cb_palette
  scale_color_brewer(
   palette=cb_palette
  ) +
 labs(
    subtitle=paste0(
      "Kruskal-Wallis, ",
      p_label(signif(kruskal.test(formula=dominant_lineage_extra_traits_discovered~con-
```

```
gsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
# coord_flip()
theme(
  legend.position="none"
)
</pre>
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position lineage_novel_task_discovery_fig



```
kruskal.test(
  formula=dominant_lineage_extra_traits_discovered~condition,
  data=summary_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

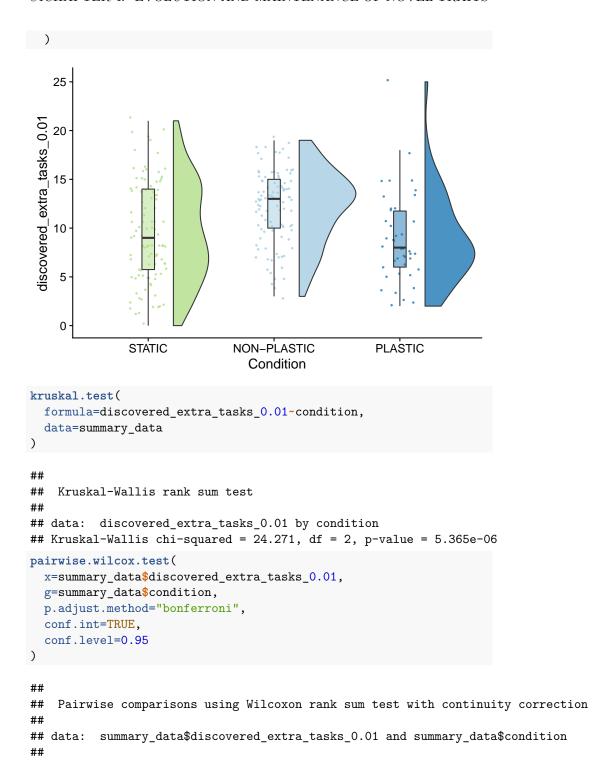
```
pairwise.wilcox.test(
  x=summary_data$dominant_lineage_extra_traits_discovered,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$dominant_lineage_extra_traits_discovered and summary_data$condi
##
           NON-PLASTIC PLASTIC
## PLASTIC 1.7e-05
## STATIC 0.0035
                       0.0561
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_di
  ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_dis
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_trait
  )
)
## [1] "PLASTIC median: 3.5; STATIC median: 4; NON-PLASTIC median: 6"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
   formula=dominant_lineage_extra_traits_discovered~condition,
    data=pair_data,
```

```
exact=FALSE,
  paired=FALSE
)
print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))

## [1] "STATIC<-->NON-PLASTIC: W=6319.5"
## [1] "STATIC<-->PLASTIC: W=1578"
## [1] "PLASTIC<-->NON-PLASTIC: W=3110.5"
```

4.8 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=cb_palette
  scale_color_brewer(
   palette=cb_palette
  ) +
  # coord_flip() +
 theme(
   legend.position="none"
```



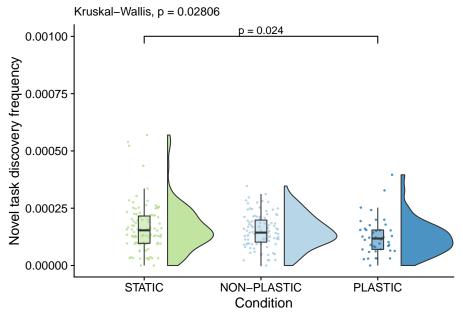
```
##
           NON-PLASTIC PLASTIC
## PLASTIC 2.4e-05
## STATIC 0.00035
                       1.00000
## P value adjustment method: bonferroni
paste(
 sep="; ",
 paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$discovered_extra_tasks_0.01)
 ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$discovered_extra_tasks_0.01)
 ),
 paste0(
   "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$discovered_extra_tasks_0.01)
 )
)
## [1] "PLASTIC median: 8; STATIC median: 9; NON-PLASTIC median: 13"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
   formula=discovered_extra_tasks_0.01~condition,
   data=pair_data,
   exact=FALSE,
   paired=FALSE
 )
 print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=6573.5"
## [1] "STATIC<-->PLASTIC: W=1918.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=3096"
```

4.9 Novel task discovery frequency (lineage)

```
summary_data$dominant_lineage_extra_traits_discovered_per_generation <- summary_data$d
summary_data$dominant_lineage_extra_traits_generations_per_discovery <- summary_data$d
# Compute manual labels for geom_signif
# stat.test <- filter(summary_data, dominant_lineage_extra_traits_discovered > 0) %>%
   wilcox test(dominant lineage extra traits generations per discovery ~ condition) %
   adjust_pvalue(method = "bonferroni") %>%
   add significance() %>%
   add_xy_position(x="condition") # ,step.increase=1
stat.test <- summary_data %>%
  wilcox_test(dominant_lineage_extra_traits_discovered_per_generation ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
  add_xy_position(x="condition", step.increase=0.0001) # , step.increase=1
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test$manual_position <- stat.test$y.position #* c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
lineage_novel_task_discovery_freq_fig <- ggplot(</pre>
    # filter(summary_data, dominant_lineage_extra_traits_discovered > 0),
    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("Novel task discovery frequency") +
```

```
scale_fill_brewer(
 palette=cb_palette
) +
scale_color_brewer(
  palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
   p_label(signif(kruskal.test(formula=dominant_lineage_extra_traits_discovered_per_generation)
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
 manual=TRUE,
 inherit.aes=FALSE
# coord_flip() +
theme(
  legend.position="none"
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
lineage_novel_task_discovery_freq_fig



```
kruskal.test(
  formula=dominant_lineage_extra_traits_discovered_per_generation~condition,
  data=summary_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=summary_data$dominant_lineage_extra_traits_discovered_per_generation,
  g=summary_data$condition,
 p.adjust.method="bonferroni",
 conf.int=TRUE,
  conf.level=0.95
)
```

Pairwise comparisons using Wilcoxon rank sum test with continuity correction

##
data: summary_data\$dominant_lineage_extra_traits_discovered_per_generation and sum
##
NON-PLASTIC PLASTIC
PLASTIC 0.092 -

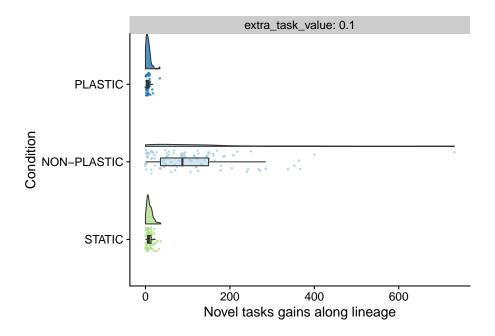
##

```
## STATIC 1.000
                     0.025
## P value adjustment method: bonferroni
paste(
 sep="; ",
 paste0(
   "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_discovered_pe
 ),
 paste0(
   "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_discovered_per
 ),
 paste0(
   "NON-PLASTIC median: ",
   median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_discovered
 )
)
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
 pair_data$condition <- as.factor(pair_data$condition)</pre>
 wt <- wilcox.test(
   formula=dominant_lineage_extra_traits_discovered_per_generation~condition,
   data=pair data,
   exact=FALSE,
   paired=FALSE
 print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=4751"
## [1] "STATIC<-->PLASTIC: W=1510.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=2584"
```

Novel tasks gained (lineage)

```
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("Novel tasks gains along lineage") +
  scale_fill_brewer(
   palette=cb_palette
 ) +
 scale_color_brewer(
   palette=cb_palette
  ) +
 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
```



4.11 Novel task loss (lineage)

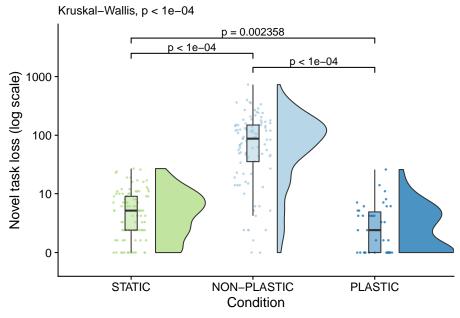
```
# Compute manual labels for geom_signif
stat.test <- summary_data %>%
  wilcox_test(dominant_lineage_extra_traits_lost ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition", step.increase=1)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- log10(stat.test$y.position) * c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
lineage_novel_task_loss_fig <- ggplot(</pre>
    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,
 labels=condition_order
) +
scale_y_continuous(
  name="Novel task loss (log scale)",
  trans=pseudo_log_trans(sigma=1, base=10),
  breaks=c(0,10,100,1000),
 limits=c(-1,5000)
scale_fill_brewer(
 palette=cb_palette
) +
scale_color_brewer(
 palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_extra_traits_lost~condition
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj<=alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
 manual=TRUE,
 inherit.aes=FALSE
) +
# coord_flip()
theme(
  legend.position="none"
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position

lineage_novel_task_loss_fig

##



```
kruskal.test(
  formula=dominant_lineage_extra_traits_lost~condition,
  data=summary_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=summary_data$dominant_lineage_extra_traits_lost,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
```

Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
data: summary_data\$dominant_lineage_extra_traits_lost and summary_data\$condition
##

```
##
           NON-PLASTIC PLASTIC
## PLASTIC 2.7e-16
## STATIC < 2e-16
                       0.0024
## P value adjustment method: bonferroni
paste(
 sep="; ",
  paste0(
    "PLASTIC median: ",
   median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_loc
 ),
  paste0(
    "STATIC median: ",
   median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_los
  ),
  paste0(
   "NON-PLASTIC median: ",
    median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_trait
  )
)
## [1] "PLASTIC median: 2; STATIC median: 5; NON-PLASTIC median: 87.5"
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
 pair_data <- filter(summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
    formula=dominant_lineage_extra_traits_lost~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
  )
 print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=9105"
## [1] "STATIC<-->PLASTIC: W=1353.5"
## [1] "PLASTIC<-->NON-PLASTIC: W=3959"
```

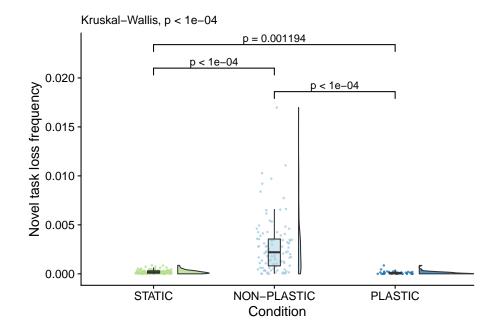
ylab("Novel task loss frequency") +

4.12 Frequency of novel task loss (lineage)

```
summary_data$dominant_lineage_extra_traits_lost_per_generation <- summary_data$dominant_lineage_e
summary_data$dominant_lineage_extra_traits_generations_per_loss <- summary_data$dominant_generations_
# Compute manual labels for geom_signif
\# stat.test <- filter(summary_data, dominant_lineage_extra_traits_lost > 0) %>%
# wilcox_test(dominant_lineage_extra_traits_generations_per_loss ~ condition) %>%
# adjust_pvalue(method = "bonferroni") %>%
# add significance() %>%
# add_xy_position(x="condition", step.increase=1)
stat.test <- summary_data %>%
  wilcox_test(dominant_lineage_extra_traits_lost_per_generation ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition", step.increase=.1)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in g
\text{stat.test\$manual\_position} \leftarrow \text{stat.test\$y.position} \ \#* \ c(1.0,1.0,1.03)
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
lineage_novel_task_loss_freq_fig <- ggplot(</pre>
    # filter(summary_data, dominant_lineage_extra_traits_lost > 0),
    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
  ) +
  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=cb_palette
scale_color_brewer(
  palette=cb_palette
) +
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_extra_traits_lost_per_gener
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj<=alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
  manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
lineage_novel_task_loss_freq_fig



```
kruskal.test(
     formula=dominant_lineage_extra_traits_lost_per_generation~condition,
     data=summary_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=summary_data$dominant_lineage_extra_traits_lost_per_generation,
     g=summary_data$condition,
     p.adjust.method="bonferroni",
     conf.int=TRUE,
     conf.level=0.95
)
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$dominant_lineage_extra_traits_lost_per_generation and summary_data$condit
##
                              NON-PLASTIC PLASTIC
##
## PLASTIC 1.1e-15
## STATIC < 2e-16
                                                               0.0012
## P value adjustment method: bonferroni
paste(
     sep="; ",
     paste0(
           "PLASTIC median: ",
          median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_extra_traits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_per_general_near_state_attraits_lost_
     ),
     paste0(
           "STATIC median: ",
          median(filter(summary_data, condition=="STATIC")$dominant_lineage_extra_traits_lost_per_gener
     ),
     paste0(
           "NON-PLASTIC median: ",
          median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_extra_traits_lost_per_
     )
)
```

[1] "PLASTIC median: 6.25141973661864e-05; STATIC median: 0.000161396283669756; NON-PLASTIC median: 0.000161396283669756;

```
print("Wilcox rank sum test statistics:")

## [1] "Wilcox rank sum test statistics:"

for (pair in pairwise_comparisons) {
    pair_data <- filter(summary_data, condition %in% pair)
    pair_data$condition <- as.factor(pair_data$condition)
    wt <- wilcox.test(
        formula=dominant_lineage_extra_traits_lost_per_generation~condition,
        data=pair_data,
        exact=FALSE,
        paired=FALSE
    )
    print(pasteO(pair[1], "<-->", pair[2], ": W=",wt$statistic))
}

## [1] "STATIC<-->NON-PLASTIC: W=8940"

## [1] "STATIC<-->PLASTIC: W=1311"

## [1] "PLASTIC<-->NON-PLASTIC: W=3922"
```

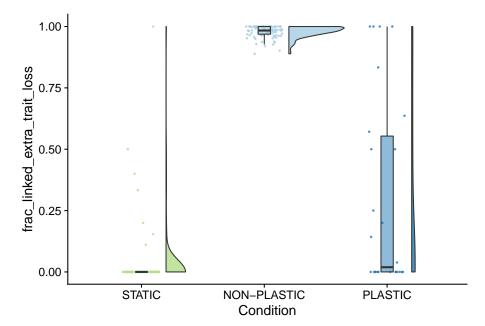
4.13 How many instances of novel trait loss cooccurred with changes in base phenotype?

Task loss linked with primary trait changes.

```
lost_traits_summary_data <- filter(summary_data, extra_task_value==0.1 & dominant_line)
lost_traits_summary_data$frac_linked_extra_trait_loss <- lost_traits_summary_data$dominant_line)</pre>
```

```
ggplot(lost_traits_summary_data, aes(x=condition, y=frac_linked_extra_trait_loss, 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,
   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=cb_palette
) +
scale_color_brewer(
  palette=cb_palette
) +
# coord_flip() +
theme(
  legend.position="none"
)
```



```
kruskal.test(
  formula=frac_linked_extra_trait_loss~condition,
  data=lost_traits_summary_data
)

##

## Kruskal-Wallis rank sum test

##

## 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,</pre>
```

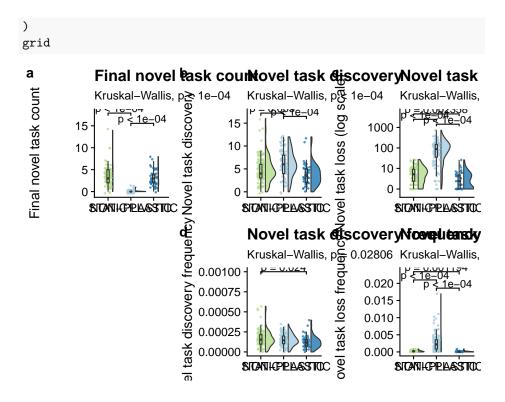
```
g=lost_traits_summary_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: lost_traits_summary_data$frac_linked_extra_trait_loss and lost_traits_summary
##
##
           NON-PLASTIC PLASTIC
## PLASTIC 1.9e-08
## STATIC < 2e-16
                       1.8e-06
##
## P value adjustment method: bonferroni
paste(
  sep="; ",
  paste0(
    "PLASTIC median: ",
    median(filter(lost_traits_summary_data, condition=="PLASTIC")$frac_linked_extra_traits_summary_data
  paste0(
    "STATIC median: ",
    median(filter(lost_traits_summary_data, condition=="STATIC")$frac_linked_extra_tra
  ),
  paste0(
    "NON-PLASTIC median: ",
    median(filter(lost_traits_summary_data, condition=="NON-PLASTIC")$frac_linked_extra
)
## [1] "PLASTIC median: 0.0192307692307692; STATIC median: 0; NON-PLASTIC median: 0.98
print("Wilcox rank sum test statistics:")
## [1] "Wilcox rank sum test statistics:"
for (pair in pairwise_comparisons) {
  pair_data <- filter(lost_traits_summary_data, condition %in% pair)</pre>
  pair_data$condition <- as.factor(pair_data$condition)</pre>
  wt <- wilcox.test(
    formula=frac_linked_extra_trait_loss~condition,
    data=pair_data,
    exact=FALSE,
    paired=FALSE
```

```
print(paste0(pair[1], "<-->", pair[2], ": W=",wt$statistic))
## [1] "STATIC<-->NON-PLASTIC: W=8344"
## [1] "STATIC<-->PLASTIC: W=1602"
## [1] "PLASTIC<-->NON-PLASTIC: W=2212"
sum(filter(lost_traits_summary_data, condition=="NON-PLASTIC")$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_lin
## [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_traits_lost)
## [1] 631
aggregate_frac_linked_extra_trait_loss_nonplastic <- sum(filter(lost_traits_summary_data, condition))
{\tt aggregate\_frac\_linked\_extra\_trait\_loss\_nonplastic}
## [1] 0.02060222
```

4.14 Manuscript figures

4.15 Combined panel

```
grid <- plot_grid(</pre>
 final_novel_task_count_fig +
    theme(
      axis.title.x=element blank()
    ggtitle("Final novel task count"),
 lineage_novel_task_discovery_fig +
      axis.title.x=element_blank(),
      # axis.text.x=element_blank(),
      # axis.ticks.x=element_blank()
    ggtitle("Novel task discovery"),
 lineage_novel_task_loss_fig +
    theme(
      axis.title.x=element_blank(),
      # axis.text.x=element_blank(),
      # axis.ticks.x=element blank()
   ) +
    ggtitle("Novel task loss"),
 NULL,
 lineage_novel_task_discovery_freq_fig +
    theme(
      axis.title.x=element_blank()
    ) +
    ggtitle("Novel task discovery frequency"),
 lineage_novel_task_loss_freq_fig +
    theme(
      axis.title.x=element_blank()
    ) +
    ggtitle("Novel task loss frequency"),
 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
```



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Chapter 5

Accumulation of deleterious instructions

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

5.1 Overview

```
total_updates <- 2000000
replicates <- 100
alpha <- 0.05
focal_poison_penalty <- 0.1

focal_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/2021-02-05-hitchhiking/analysis/" # << For bookdown
# working_directory <- "./"</pre>
```

5.2 Analysis dependencies

Load all required R libraries.

```
library(RColorBrewer)
library(ggplot2)
library(rstatix)
```

```
library(ggsignif)
library(scales)
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
## minor
                0.5
                2021
## year
## month
                03
## day
                 31
                80133
## svn rev
## language
                 R
## version.string R version 4.0.5 (2021-03-31)
## nickname
               Shake and Throw
```

5.3 Setup

```
###### summary data ######
summary_data_loc <- pasteO(working_directory, "data/aggregate.csv")
summary_data <- read.csv(summary_data_loc, na.strings="NONE")

summary_data$DISABLE_REACTION_SENSORS <- as.factor(summary_data$DISABLE_REACTION_SENSORS
summary_data$chg_env <- summary_data$chg_env == "True"
summary_data$dominant_plastic_odd_even <- as.factor(summary_data$dominant_plastic_odd_even summary_data$sensors <- summary_data$DISABLE_REACTION_SENSORS == "0"
summary_data$is_plastic <- summary_data$dominant_plastic_odd_even == "True"
summary_data$POISON_PENALTY <- as.factor(summary_data$POISON_PENALTY)

summary_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation <</pre>
```

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summary_data\$frac_hitchhiking_linked_trait_change <- summary_data\$dominant_lineage_num_times_hitchhiker 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_inc

```
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(
```

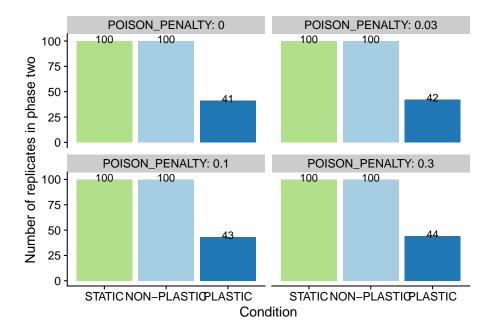
```
"STATIC",
 "NON-PLASTIC",
 "PLASTIC"
pairwise_comparisons <- list(</pre>
  c("STATIC", "NON-PLASTIC"),
  c("STATIC", "PLASTIC"),
  c("PLASTIC", "NON-PLASTIC")
)
p_label <- function(p_value) {</pre>
  threshold = 0.0001
  if (p_value < threshold) {</pre>
    return(paste0("p < ", threshold))</pre>
  } else {
    return(paste0("p = ", p_value))
  }
poison_penalties <- levels(summary_data$POISON_PENALTY)</pre>
##### time series #####
lineage time series data loc <- pasteO(working directory, "data/lineage series.csv")
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_data)</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</pre>
lineage_time_series_data$POISON_PENALTY <- as.factor(lineage_time_series_data$POISON_V.
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
focal_summary_data <- filter(summary_data, POISON_PENALTY==focal_poison_penalty)
theme_set(theme_cowplot())
cb_palette <- "Paired"
dir.create(pasteO(working_directory, "plots"), showWarnings=FALSE)
samplemean <- function(x, d) {
   return(mean(x[d]))
}</pre>
```

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

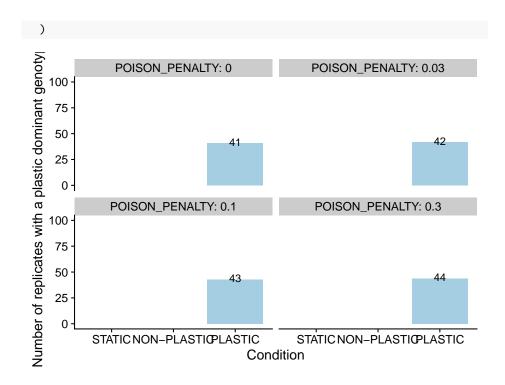


We can confirm our expectation that the dominant genotypes in non-plastic conditions are not phenotypically plastic.

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

`summarise()` has grouped output by 'condition', 'is_plastic'. You can override using ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition, y=n, fill=conditi

```
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=cb_palette
) +
scale_color_brewer(
   palette=cb_palette
) +
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

```
names(occurrences) <- c(</pre>
    "NON-PLASTIC",
    "PLASTIC",
    "STATIC"
  poison_exec_table <- data.frame(</pre>
    executes.poison=occurrences,
    replicates=trials
  cat(paste0("#### Penalty: ", penalty, "\n"))
  cat(print(kable(poison_exec_table)))
  cat("\n")
  ft <- pairwise.fisher.test(x=occurrences, n=trials, p.adjust.method="bonferroni")</pre>
  print(ft)
  cat("\n\n")
## #### Penalty: 0
##
## \begin{tabular}{||r|r}
## \hline
## & executes.poison & replicates\\
## \hline
## NON-PLASTIC & 86 & 100\\
## \hline
## PLASTIC & 27 & 41\\
## \hline
## STATIC & 85 & 100\\
## \hline
## \end{tabular}
##
##
## Pairwise comparisons using Pairwise comparison of proportions (Fisher)
##
## data: occurrences out of trials
           NON-PLASTIC PLASTIC
## PLASTIC 0.03
## STATIC 1.00
                       0.06
## P value adjustment method: bonferroni
##
##
## #### Penalty: 0.03
##
```

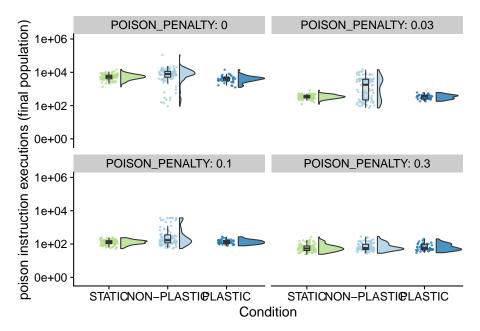
```
## \begin{tabular}{l|r|r}
## \hline
    & executes.poison & replicates\\
## \hline
## NON-PLASTIC & 46 & 100\\
## \hline
## PLASTIC & 1 & 42\\
## \hline
## STATIC & 1 & 100\\
## \hline
## \end{tabular}
##
## Pairwise comparisons using Pairwise comparison of proportions (Fisher)
## data: occurrences out of trials
##
          NON-PLASTIC PLASTIC
## PLASTIC 1.2e-07
## STATIC 2.9e-15
                   1
## P value adjustment method: bonferroni
##
## #### Penalty: 0.1
## \begin{tabular}{l|r|r}
## \hline
## & executes.poison & replicates\\
## \hline
## NON-PLASTIC & 14 & 100\\
## \hline
## PLASTIC & 0 & 43\\
## \hline
## STATIC & 0 & 100\\
## \hline
## \end{tabular}
##
##
## 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
##
##
## #### Penalty: 0.3
##
## \begin{tabular}{||r|r}
## \hline
    & executes.poison & replicates\\
## \hline
## NON-PLASTIC & 0 & 100\\
## \hline
## PLASTIC & 0 & 44\\
## \hline
## STATIC & 0 & 100\\
## \hline
## \end{tabular}
##
##
##
   Pairwise comparisons using Pairwise comparison of proportions (Fisher)
##
## data: occurrences out of trials
          NON-PLASTIC PLASTIC
## PLASTIC 1
## STATIC 1
## P value adjustment method: bonferroni
```

5.5.2 Poison instruction execution (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_trans(sigma=1,base=10),
  breaks=c(0,100,10000,1000000),
  limits=c(-1,1000000)
) +
scale_fill_brewer(
  palette=cb_palette
) +
scale_color_brewer(
  palette=cb_palette
) +
facet_wrap(
  ~POISON_PENALTY,
  labeller=label_both
) +
# coord_flip() +
theme(
  legend.position="none"
ggsave(
  paste0(working_directory, "plots/final-population-poison-log.pdf"),
  width=15,
  height=10
)
```



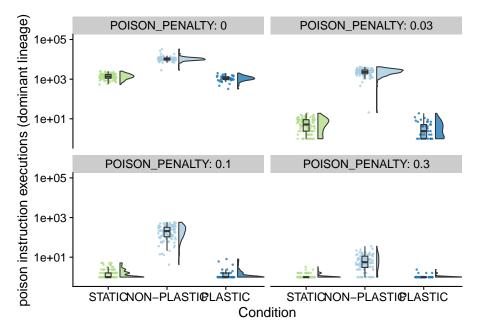
```
for (penalty in poison_penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)</pre>
  print(
    paste0(
      "PENALTY: ", penalty
    )
  )
  kt <- kruskal.test(</pre>
      formula=final_population_poison~condition,
      data=stat_data
    )
  print(
    kt
  )
  if (is.na(kt$p.value)) { next }
  if (kt$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 Cummulative poison instruction execution along final dominant lineages

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_times_poison_executed, 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
 ) +
 scale_y_continuous(
   name="poison instruction executions (dominant lineage)",
   trans=pseudo_log_trans(sigma = 1, base = 10),
   breaks=c(10,1000,100000),
   limits=c(-1,100000)
 ) +
 facet_wrap(
   ~POISON PENALTY,
   labeller=label_both
```

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



```
for (penalty in poison_penalties) {
  stat_data <- filter(summary_data, POISON_PENALTY==penalty)
  print(
    paste0(
        "PENALTY: ", penalty
    )
  )
  kt <- kruskal.test(
        formula=dominant_lineage_times_poison_executed~condition,
        data=stat_data</pre>
```

```
)
 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

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec
 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
 ) +
 facet_wrap(
    ~POISON_PENALTY,
   labeller=label_both
 ) +
 scale_fill_brewer(
   palette=cb_palette
 ) +
 scale_color_brewer(
   palette=cb_palette
 ) +
 theme(
   legend.position="none"
```

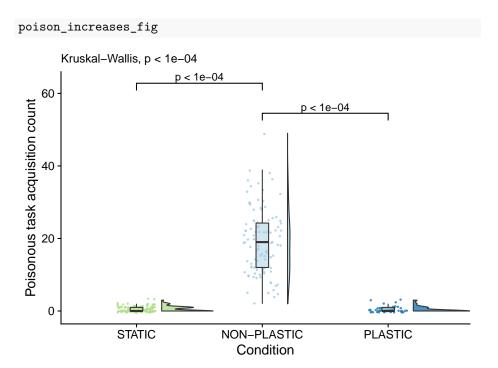
```
ninant_lineage_num_times_hitchhike_inst_exec_incr
              POISON_PENALTY: 0
                                               POISON_PENALTY: 0.03
   200
   150
    100
    50
     0 -
             POISON_PENALTY: 0.1
                                               POISON_PENALTY: 0.3
   200
   150
   100
    50
     0 -
          STATICNON-PLASTICPLASTIC
                                            STATICNON-PLASTICPLASTIC
                                    Condition
for (penalty in poison_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$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_
##
          NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
## STATIC < 2e-16
                      0.00046
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.03"
## Kruskal-Wallis rank sum test
##
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases by condition
## Kruskal-Wallis chi-squared = 179.35, df = 2, p-value < 2.2e-16
##
##
## Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_
##
##
          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_
##
```

```
##
           NON-PLASTIC PLASTIC
## PLASTIC <2e-16
## STATIC <2e-16
                       0.27
## 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$dominant_lineage_num_times_hitchhike_inst_exec_increases and stat_data$condit
##
           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)$dominant_lineage_num_
\# sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)\#dominant_lineage_num_times
# sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_lineage_num_times_
Focal figure for the manuscript:
# Compute manual labels for geom_signif
stat.test <- focal_summary_data %>%
  wilcox_test(dominant_lineage_num_times_hitchhike_inst_exec_increases ~ condition) %>%
  adjust_pvalue(method = "bonferroni") %>%
  add_significance() %>%
  add_xy_position(x="condition")
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- stat.test$y.position</pre>
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
poison_increases_fig <- ggplot(</pre>
   focal_summary_data,
    aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases, 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="Poisonous task acquisition count",
scale_fill_brewer(
  palette=cb_palette
scale_color_brewer(
 palette=cb_palette
# coord_flip()
labs(
  subtitle=paste0(
    "Kruskal-Wallis, ",
    p_label(signif(kruskal.test(formula=dominant_lineage_num_times_hitchhike_inst_ex
  )
) +
ggsignif::geom_signif(
  data=filter(stat.test, p.adj <= alpha),</pre>
  aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
 manual=TRUE,
  inherit.aes=FALSE
) +
theme(
  legend.position="none"
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position



5.6.2 Frequency of increases in poison instruction execution (lineage)

```
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=cb_palette
  ) +
  scale_color_brewer(
    palette=cb_palette
  ) +
  facet_wrap(
    ~POISON_PENALTY,
    labeller=label_both,
    scales="free_y"
  ) +
  # coord_flip() +
  theme(
    legend.position="none"
  ) +
  ggsave(
    paste0(working_directory, "plots/final-dominant-lineage-poison-increase-per-general
    width=15,
    height=10
  )
neage_num_times_hitchhike_inst_exec_increases_p
              POISON_PENALTY: 0
                                                 POISON_PENALTY: 0.03
                                        0.005
   0.005
                                        0.004
   0.004
   0.003
                                        0.003
   0.002
                                        0.002
   0.001
                                        0.001
   0.000 -
                                        0.000 -
             POISON_PENALTY: 0.1
                                                  POISON_PENALTY: 0.3
                                        0.005
   0.005
   0.004
                                        0.004
   0.003
                                        0.003
   0.002
                                        0.002
   0.001
                                        0.001
   0.000
                                        0.000
            STATIGION-PLASTIC
                                                STATICION-PLASTICLASTIC
                                     Condition
for (penalty in poison_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~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$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation,
      g=stat_data$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 s
##
          NON-PLASTIC PLASTIC
## PLASTIC < 2e-16
## STATIC < 2e-16
                      7.8e-05
## 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$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_gener
##
          NON-PLASTIC PLASTIC
##
## PLASTIC <2e-16
## STATIC <2e-16
                       0.019
##
## P value adjustment method: bonferroni
## [1] "PENALTY: 0.1"
##
##
   Kruskal-Wallis rank sum test
##
## data: dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation by c
## Kruskal-Wallis chi-squared = 184.17, df = 2, p-value < 2.2e-16
##
##
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: stat_data$dominant_lineage_num_times_hitchhike_inst_exec_increases_per_gener
##
          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
```

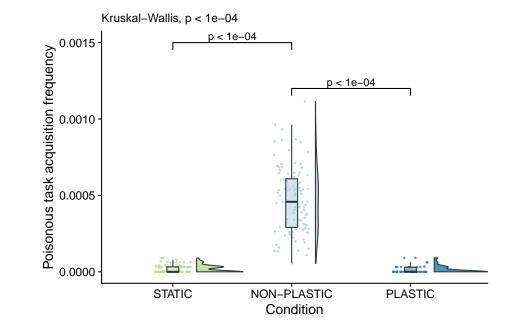
Figure for the manuscript:

```
# Compute manual labels for geom_signif
stat.test <- focal_summary_data %>%
  wilcox_test(dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation ~ condition
  adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
 add_xy_position(x="condition", step.increase=0.2)
# Tweak y.position manually to account for scaled axis (edge case that triggers bad behavior in
stat.test$manual_position <- stat.test$y.position</pre>
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
poison_increases_per_gen_fig <- ggplot(</pre>
    focal_summary_data,
    aes(x=condition, y=dominant_lineage_num_times_hitchhike_inst_exec_increases_per_generation, 1
  ) +
  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="Poisonous task acquisition frequency",
  scale_fill_brewer(
    palette=cb_palette
  scale_color_brewer(
    palette=cb_palette
  ) +
  # coord_flip()
```

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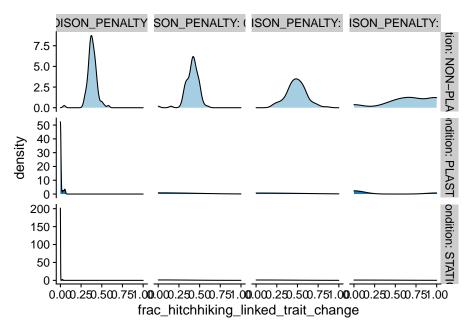
```
labs(
    subtitle=paste0(
        "Kruskal-Wallis, ",
        p_label(signif(kruskal.test(formula=dominant_lineage_num_times_hitchhike_inst_ext)
)
) +
ggsignif::geom_signif(
    data=filter(stat.test, p.adj <= alpha),
    aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
    manual=TRUE,
    inherit.aes=FALSE
) +
theme(
    legend.position="none"</pre>
```

Warning: Ignoring unknown aesthetics: xmin, xmax, annotations, y_position
poison_increases_per_gen_fig

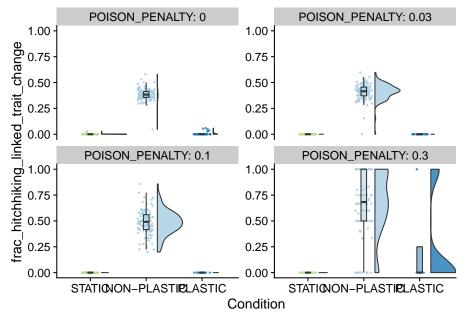


5.6.3 What fraction of mutations that increase poison instruction execution co-occur with base trait changes?

```
ggplot(filter(summary_data, dominant_lineage_num_times_hitchhike_inst_exec_increases>0), aes(x=filter)
 geom_density() +
 facet_grid(
   condition~POISON_PENALTY,
   labeller=label_both,
   scales="free_y"
  scale_fill_brewer(
   palette=cb_palette
  scale_color_brewer(
   palette=cb_palette
  ) +
 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
  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=cb_palette
 ) +
  scale_color_brewer(
    palette=cb_palette
```



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
```

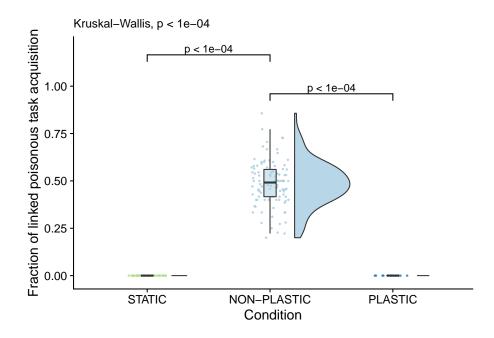
##

```
## 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)$dominant_lineag
num <- sum(filter(summary_data, condition=="NON-PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_
paste0("NON-PLASTIC (0.1 penalty): ", num/denom, "(", num, "/", denom, ")")
## [1] "NON-PLASTIC (0.1 penalty): 0.498956158663883(956/1916)"
denom <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_nu
num <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_num_
paste0("PLASTIC (0.1 penalty): ", num/denom, " (", num, "/", denom, ")")
## [1] "PLASTIC (0.1 penalty): 0 (0/18)"
```

```
denom <- sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_
num <- sum(filter(summary_data, condition=="STATIC" & POISON_PENALTY==0.1)$dominant_li</pre>
paste0("STATIC (0.1 penalty): ", num/denom, " (", num, "/", denom, ")")
## [1] "STATIC (0.1 penalty): 0 (0/58)"
Focal figure for the manuscript:
# Compute manual labels for geom_signif
stat.test <-filter(focal_summary_data,dominant_lineage_num_times_hitchhike_inst_exec_i:
  wilcox_test(frac_hitchhiking_linked_trait_change ~ condition, comparisons=list(c("PL
 adjust_pvalue(method = "bonferroni") %>%
 add_significance() %>%
 add xy position(x="condition")
# Tweak y.position manually to account for scaled axis (edge case that triggers bad be
stat.test$manual_position <- stat.test$y.position</pre>
stat.test$label <- mapply(p_label,stat.test$p.adj)</pre>
linked_trait_change_fig <- ggplot(</pre>
    filter(focal_summary_data, dominant_lineage_num_times_hitchhike_inst_exec_increase
    aes(x=condition, y=frac_hitchhiking_linked_trait_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="Fraction of linked poisonous task acquisition",
    limits=c(-0.01, 1.2),
    breaks=c(0, 0.25, 0.50, 0.75, 1.0)
```

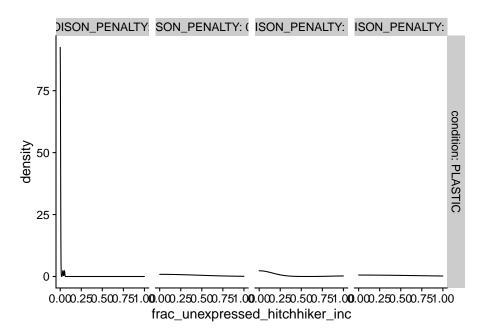
5.6. CHARACTERIZING MUTATIONS THAT INCREASE POISON INSTRUCTION EXECUTION139

```
) +
        scale_fill_brewer(
               palette=cb_palette
        scale_color_brewer(
                   palette=cb_palette
        labs(
                    subtitle=paste0(
                             "Kruskal-Wallis, ",
                              p_label(signif(kruskal.test(formula=frac_hitchhiking_linked_trait_change~condition, data=formula=frac_hitchhiking_linked_trait_change~condition, data=formula=frac_hitchhiking_linked_trait_change~condition, data=formula=frac_hitchhiking_linked_trait_change~condition, data=formula=frac_hitchhiking_linked_trait_change~condition, data=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=formula=f
                    )
        ) +
        ggsignif::geom_signif(
                    data=filter(stat.test, p.adj <= alpha),</pre>
                    aes(xmin=group1,xmax=group2,annotations=label,y_position=manual_position),
                   manual=TRUE,
                    inherit.aes=FALSE
        ) +
         theme(
                    legend.position="none"
```



5.7 What fraction of poison execution increases

```
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"
    ) +
    theme(
        legend.position="none"
    )
```



```
denom <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_nu
num <- sum(filter(summary_data, condition=="PLASTIC" & POISON_PENALTY==0.1)$dominant_lineage_num
pasteO("PLASTIC: ", num/denom, " (", num, "/", denom, ")")</pre>
```

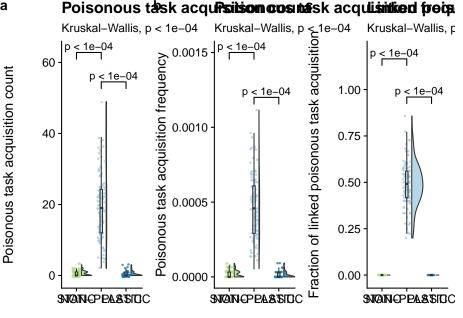
5.8 Manuscript figures

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

```
grid <- plot_grid(
  poison_increases_fig +
    theme(
       axis.title.x=element_blank()
    ) +
    ggtitle("Poisonous task acquisition count"),
  poison_increases_per_gen_fig +
    theme(
       axis.title.x=element_blank()
    ) +
    ggtitle("Poisonous task acquisition frequency"),
  linked_trait_change_fig +
    theme(
       axis.title.x=element_blank()
    ) +
    ggtitle("Linked poisonous task acquisition"),</pre>
```

```
nrow=1,
  align="v",
 labels="auto"
save_plot(
  pasteO(working_directory, "plots/", "poison-accumulation-panel.pdf"),
  base_height=6,
   base_asp=3/1
grid
```

Poisonous takk acquiraitisom cosutakk acquiraitised freig а



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
                  0.5
## minor
## year
                  2021
## month
                  03
## day
                  31
## svn rev
                  80133
## language
                  R
## version.string R version 4.0.5 (2021-03-31)
## nickname
                  Shake and Throw
```

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")
  }
}
```

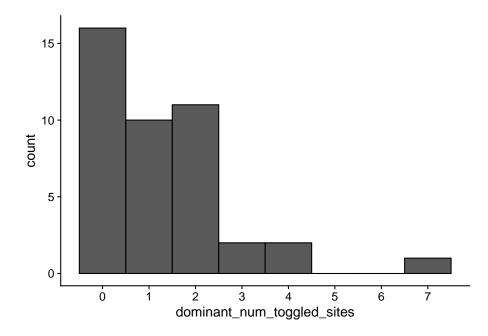
```
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
 } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
 }
}
trace_summary_data$env_label <- mapply(</pre>
  env_label_fun,
  trace_summary_data$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?

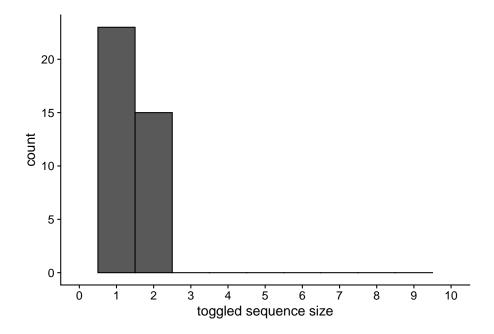
```
chunk_sizes <- data.frame(
    size=integer()
)
for (sizes in trace_summary_data$dominant_toggled_chunk_sizes) {
    if (sizes == "") { next }
        sizes <- unlist(lapply(str_split(sizes, ';'), as.integer))
        chunk_sizes <- rbind(chunk_sizes, data.frame(size=c(sizes)))
}</pre>
```

6.5. WHAT IS THE DISTRUBUTION OF TOGGLED SEQUENCE SIZES?147

```
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", "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
                  0.5
                  2021
## year
## month
                  03
## day
                  31
## svn rev
                  80133
## language
                 R
## version.string R version 4.0.5 (2021-03-31)
## nickname
                  Shake and Throw
```

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")
```

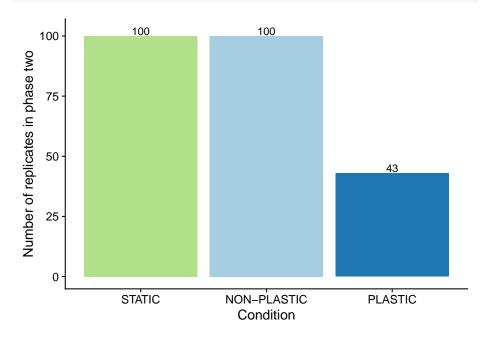
```
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
  } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
 }
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$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())
```

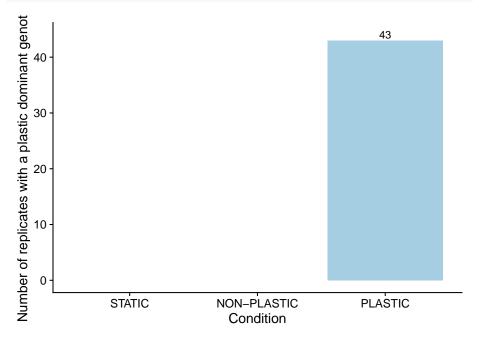
```
## `summarise()` has grouped output by 'sensors', 'env_label'. You can override using 'ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    geom_text(aes(label=n, y=n+2)) +
    scale_x_discrete(
        name="Condition",
        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())
```

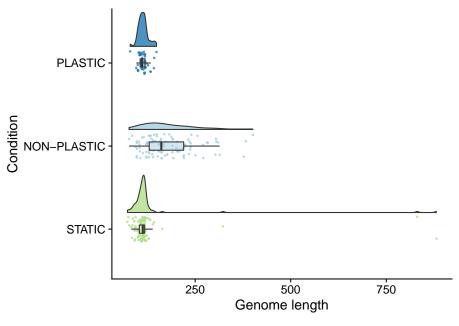
```
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
  geom_col(position=position_dodge(0.9)) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
  ) +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  )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

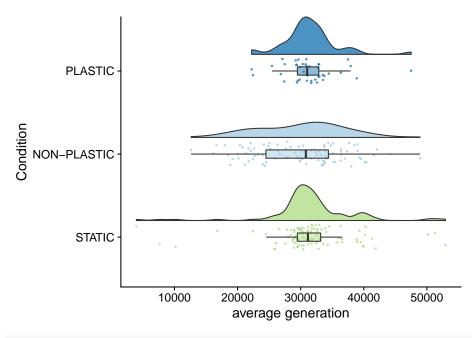
## [1] 45
median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)

## [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"
```

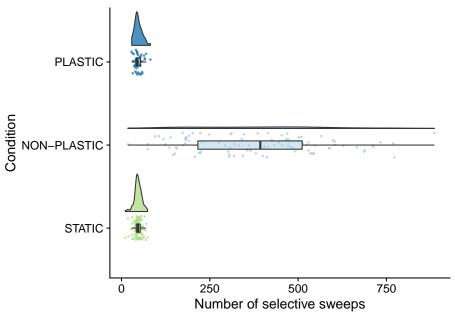


```
median(filter(summary_data, condition=="PLASTIC")$time_average_generation)
## [1] 31028.6
median(filter(summary_data, condition=="STATIC")$time_average_generation)
## [1] 31147.5
median(filter(summary_data, condition=="NON-PLASTIC")$time_average_generation)
## [1] 30817.95
kruskal.test(
  formula=time_average_generation~condition,
  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
```

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

```
PLASTIC NON-PLASTIC - 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)
)
```

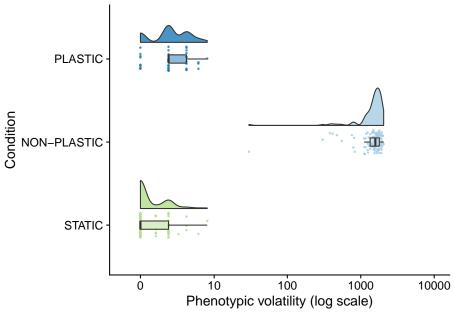
[1] "STATIC: 668.25523255814"

```
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"
```



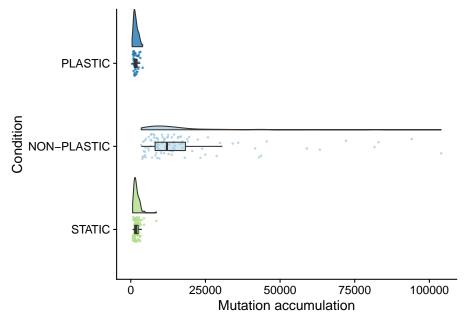
```
paste0(
  "PLASTIC: ",
  median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility)
## [1] "PLASTIC: 2"
paste0(
  "STATIC: ",
  median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility)
## [1] "STATIC: O"
paste0(
  "NON-PLASTIC: ",
  median(filter(summary_data, 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"
```

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```
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
```