Supplemental Material

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Chapter 1

Introduction

TODO

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/" # << For bookdown
# working_directory <- "./" # << 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
                  0.3
                  2020
## year
## month
                  10
                  10
## day
                  79318
## svn rev
## language
## version.string R version 4.0.3 (2020-10-10)
                  Bunny-Wunnies Freak Out
## nickname
```

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", "nonginames_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

The effect of adaptive phenotypic plasticity on evolutionary change

3.1 Overview

```
total_updates <- 200000
replicates <- 100

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

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

3.2 Analysis dependencies

Load all required R libraries.

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

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
## major
                  0.3
## minor
## year
                  2020
## month
                  10
## day
                  10
                  79318
## svn rev
## language
                  R
## version.string R version 4.0.3 (2020-10-10)
## nickname
                  Bunny-Wunnies Freak Out
```

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"
summary_data$is_plastic <- summary_data$dominant_plastic_odd_even == "True"
env_label_fun <- function(chg_env) {</pre>
  if (chg_env) {
    return("Fluctuating")
  } else {
    return("Constant")
}
sensors label fun <- function(has sensors) {</pre>
  if (has_sensors) {
    return("Sensors")
  } else {
   return("No sensors")
```

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```
}
# note that this labeler makes assumptions about how we set up our experiment
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
 } else if (env_chg) {
   return("NON-PLASTIC")
 } else {
    return("STATIC")
 }
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
summary_data$condition <- mapply(</pre>
 condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
)
condition order = c(
  "STATIC",
 "NON-PLASTIC",
  "PLASTIC"
)
##### time series ####
# time_series_data_loc <- paste0(working_directory, "data/time_series_u0-u200000.csv")
time_series_data_loc <- paste0(working_directory, "data/time_series_u95000-u105000.csv")
time_series_data <- read.csv(time_series_data_loc)</pre>
time_series_data$DISABLE_REACTION_SENSORS <- as.factor(time_series_data$DISABLE_REACTION_SENSORS)
time_series_data$chg_env <- time_series_data$chg_env == "True"</pre>
time_series_data$sensors <- time_series_data$DISABLE_REACTION_SENSORS == "0"
time_series_data$env_label <- mapply(</pre>
  env_label_fun,
```

```
time_series_data$chg_env
)
time_series_data$sensors_label <- mapply(
    sensors_label_fun,
    time_series_data$sensors
)
time_series_data$condition <- mapply(
    condition_label_fun,
    time_series_data$sensors,
    time_series_data$chg_env
)

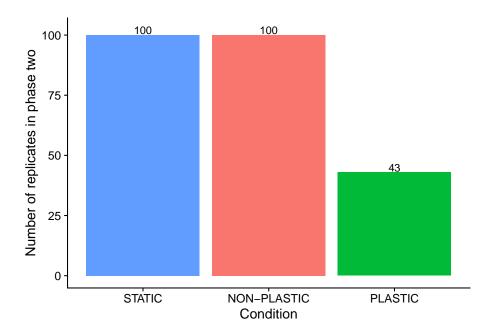
####### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)</pre>
```

3.4 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())
```

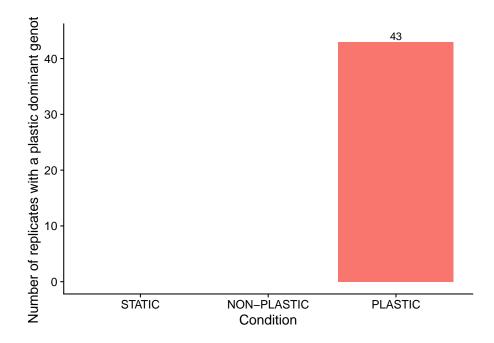
```
## `summarise()` has grouped output by 'sensors', 'env_label'. You can override using 'ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    geom_text(aes(label=n, y=n+2)) +
    scale_x_discrete(
    name="Condition",
    limits=condition_order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

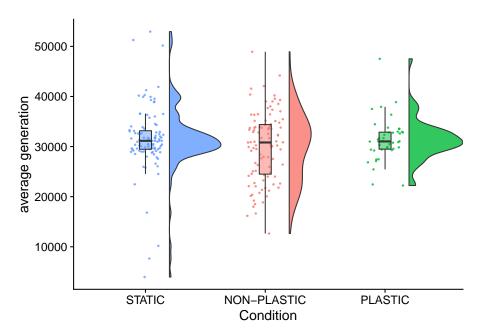
```
## `summarise()` has grouped output by 'condition'. You can override using the `.groups` argument
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    geom_text(aes(label=n, y=n+1)) +
    ylab("Number of replicates with a plastic dominant genotype") +
    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
 ylab("average generation") +
```

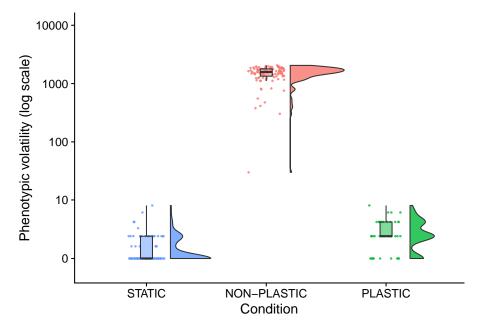
```
theme(
  legend.position="none"
)
```



```
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
```

3.6 Phenotypic volatility along dominant lineage

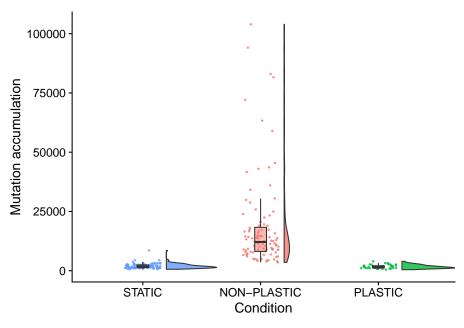
```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_trait_volatility, fill=condit
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
 geom_boxplot(
   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)
 ) +
 theme(
   legend.position="none"
```



```
median(filter(summary_data, condition=="PLASTIC")$dominant_lineage_trait_volatility)
## [1] 2
median(filter(summary_data, condition=="STATIC")$dominant_lineage_trait_volatility)
## [1] 0
median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_trait_volatility)
## [1] 1580
kruskal.test(
  formula=dominant_lineage_trait_volatility~condition,
  data=summary_data
)
##
##
   Kruskal-Wallis rank sum test
##
## data: dominant_lineage_trait_volatility by condition
## Kruskal-Wallis chi-squared = 191.98, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
 x=summary_data$dominant_lineage_trait_volatility,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
```

3.7 Mutation accumulation along the dominant

```
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
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ylab("Mutation accumulation") +
 theme(
    legend.position="none"
```



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

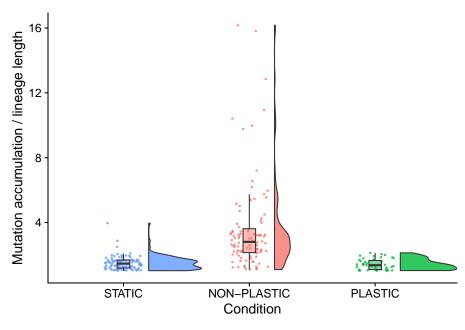
## [1] 1552
median(filter(summary_data, condition=="STATIC")$dominant_lineage_total_mut_cnt)

## [1] 1724.5
median(filter(summary_data, condition=="NON-PLASTIC")$dominant_lineage_total_mut_cnt)

## [1] 12123
```

3.7.1 Mutation accumulation normalized by lineage length

```
summary_data$mutations_per_lineage_step <- summary_data$dominant_lineage_total_mut_cnt
ggplot(summary_data, aes(x=condition, y=mutations_per_lineage_step, fill=condition)) +
 geom_flat_violin(
   position = position nudge(x = .2, y = 0),
   alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ylab("Mutation accumulation / lineage length") +
    legend.position="none"
```



```
kruskal.test(
  formula=mutations_per_lineage_step~condition,
  data=summary_data
)
##
   Kruskal-Wallis rank sum test
##
##
## data: mutations_per_lineage_step by condition
## Kruskal-Wallis chi-squared = 106.1, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=summary_data$mutations_per_lineage_step,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
)
##
   Pairwise comparisons using Wilcoxon rank sum test with continuity correction
##
## data: summary_data$mutations_per_lineage_step and summary_data$condition
##
           NON-PLASTIC PLASTIC
## PLASTIC 8.9e-14
## STATIC < 2e-16
                       0.64
##
```

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

## [1] 1.369198
median(filter(summary_data, condition=="NON-PLASTIC")$mutations_per_lineage_step)

## [1] 2.807136
median(filter(summary_data, condition=="STATIC")$mutations_per_lineage_step)

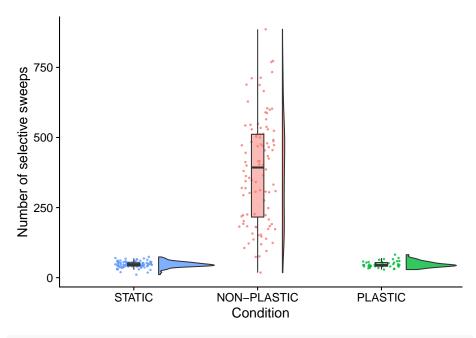
## [1] 1.464488
```

3.8 Selective sweeps

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

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

##



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

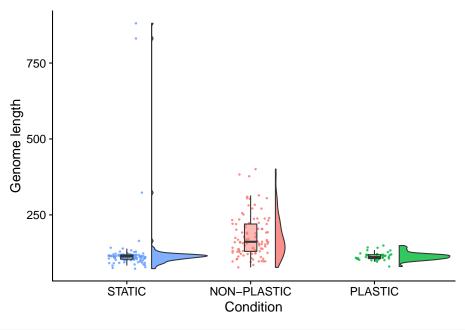
## [1] 45
median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)

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

## [1] 393
# low_mrca_change <- filter(summary_data, condition=="Non-plastic (fluctuating)" & phy</pre>
```

3.9 Genome length

```
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
 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)

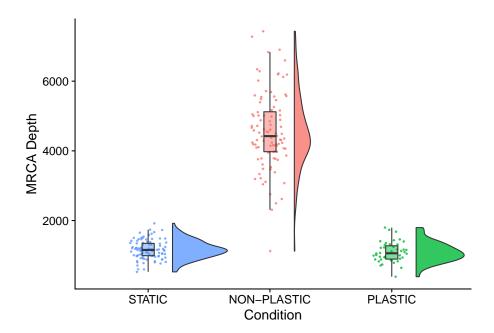
## [1] 45
median(filter(summary_data, condition=="STATIC")$phylo_mrca_changes)

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

## [1] 393
```

3.10 Depth of MRCA

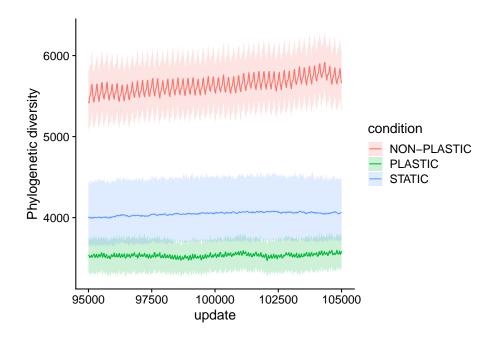
```
ggplot(summary_data, aes(x=condition, y=phylo_mrca_depth, fill=condition)) +
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(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



3.11 Phylogenetic diversity over time

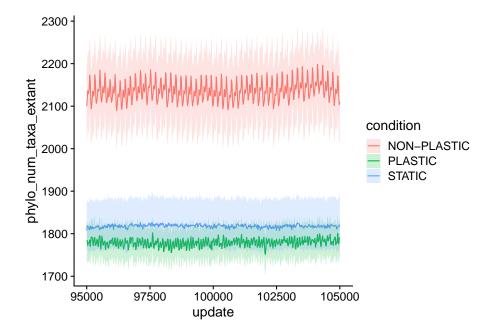
```
// From (Faith 1992, reviewed in Winters et al., 2013), phylogenetic diversity is the sum of edge
// This calculates phylogenetic diversity for all extant taxa in the tree.

ggplot(time_series_data, aes(x=update, y=phylo_current_phylogenetic_diversity, fill=condition, constat_summary(fun="mean", geom="line") +
    stat_summary(
        fun.data="mean_cl_boot",
        fun.args=list(conf.int=0.95),
        geom="ribbon",
        alpha=0.2,
        linetype=0
    ) +
    ylab("Phylogenetic diversity") +
    ggsave(
    paste0(working_directory, "plots/", "phylo-diversity-ot.png"),
        width=10,
        height=5
    )
```



3.12 Number of extant taxa (genotypes) over

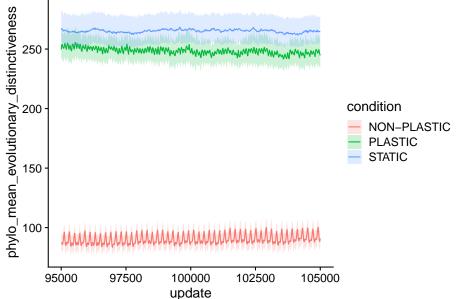
```
ggplot(time_series_data, aes(x=update, y=phylo_num_taxa_extant, fill=condition, color=stat_summary(fun="mean", geom="line") +
stat_summary(
  fun.data="mean_cl_boot",
  fun.args=list(conf.int=0.95),
  geom="ribbon",
  alpha=0.2,
  linetype=0
) +
ggsave(
  paste0(working_directory, "plots/", "phylo-num-extant-taxa-ot.png"),
  width=10,
  height=5
)
```



3.13 Evolutionary distinctiveness over time

```
/** This metric (from Isaac, 2007; reviewed in Winter et al., 2013) measures how
    * distinct @param tax is from the rest of the population, weighted for the amount of
     unique evolutionary history that it represents.
    * To quantify length of evolutionary history, this method needs @param time: the current
    * time, in whatever units time is being measured in when taxa are added to the systematics
    * manager. Note that passing a time in the past will produce innacurate results (since we
     don't know what the state of the tree was at that time).
     Assumes the tree is all connected. Will return -1 if this assumption isn't met.
ggplot(time_series_data, aes(x=update, y=phylo_mean_evolutionary_distinctiveness, fill=conditions
  stat_summary(fun="mean", geom="line") +
  stat_summary(
    fun.data="mean_cl_boot",
    fun.args=list(conf.int=0.95),
    geom="ribbon",
   alpha=0.2,
   linetype=0
  ) +
  ggsave(
```

```
paste0(working_directory, "plots/", "phylo_mean_evolutionary_distinctiveness-ot.pn,
    width=10,
    height=5
)
```



3.14 Camera-ready figures

Figures styled for the paper.

Mutation accumulation

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

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

Phenotypic volatility

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

```
) +
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 scale y continuous(
   name="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"
 ) +
 theme(
   legend.position="none",
   axis.ticks.y=element_blank(),
   axis.text.y=element_blank(),
   axis.title.y=element_blank()
 ) +
 coord_flip() +
 ggsave(
   pasteO(working_directory, "plots/", "phenotypic-volatility.pdf"),
   width=4,
   height=4
 )
```

Selective sweeps.

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

```
geom_point(
  mapping=aes(color=condition),
  position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
  width = .1,
  outlier.shape = NA,
  alpha = 0.5
scale_x_discrete(
  name="Condition",
  limits=condition_order,
  labels=condition_order
scale_y_continuous(
  name="Coalescence Events (log scale)",
  trans="log10"
) +
scale_fill_brewer(
  palette="Paired"
) +
scale_color_brewer(
  palette="Paired"
theme(
  legend.position="none",
  axis.ticks.y=element blank(),
  axis.text.y=element_blank(),
  axis.title.y=element_blank()
) +
coord_flip() +
ggsave(
  pasteO(working_directory, "plots/", "selective-sweeps.pdf"),
  width=4,
  height=4
)
```

All together

```
grid <- plot_grid(
  mutation_count_fig,
  phenotypic_volatility_fig,
  selective_sweeps_fig,
  nrow=1,</pre>
```

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

Chapter 4

Effect of phenotypic plasticity on the evolution and maintenance of complex features

4.1 Overview

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

```
"logic_3bh","logic_3bi","logic_3bj",
  "logic_3bk","logic_3bb","logic_3bm",
  "logic_3bn","logic_3bo","logic_3bs",
  "logic_3bt","logic_3bv","logic_3bv",
  "logic_3bt","logic_3bx","logic_3by",
  "logic_3bz","logic_3ca","logic_3cb",
  "logic_3cc","logic_3cd","logic_3ce",
  "logic_3cf","logic_3cg","logic_3ch",
  "logic_3ci","logic_3cj","logic_3ck",
  "logic_3ci","logic_3cm","logic_3cn",
  "logic_3co","logic_3cp"
)

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

4.2 Analysis dependencies

Load all required R libraries.

```
library(ggplot2)
library(tidyverse)
library(cowplot)
library(RColorBrewer)
library(Hmisc)
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
## minor
                  0.3
## year
                  2020
## month
                  10
## day
                  10
## svn rev
                  79318
```

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```
## language R
## version.string R version 4.0.3 (2020-10-10)
## nickname Bunny-Wunnies Freak Out
```

4.3 Setup

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

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

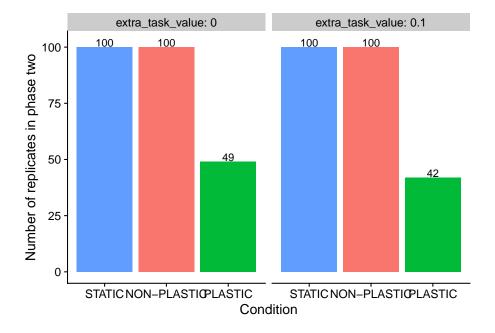
```
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)
```

4.4 Evolution of phenotypic plasticity

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

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

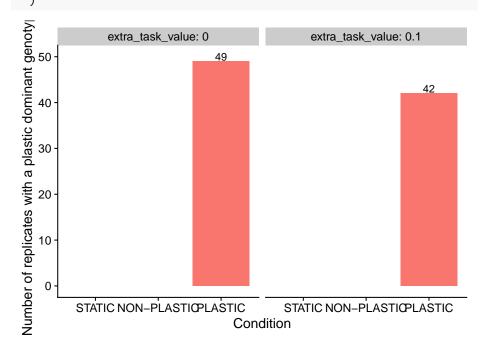
```
## `summarise()` has grouped output by 'sensors', 'env_label', 'condition'. You can override using
ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    geom_text(aes(label=n, y=n+2)) +
    scale_x_discrete(
        name="Condition",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



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

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

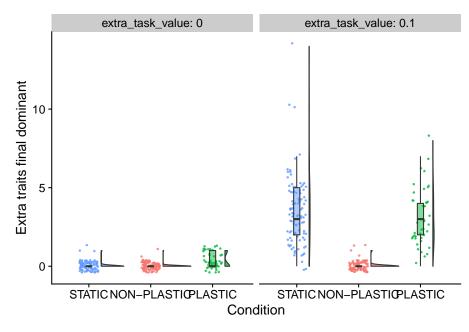
```
## `summarise()` has grouped output by 'condition', 'is_plastic'. You can override using
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition_color_col(position=position_dodge(0.9)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    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 dominant task performance

```
ggplot(summary_data, aes(x=condition, y=dominant_extra_tasks, fill=condition)) +
  geom_flat_violin(
```

```
position = position_nudge(x = .2, y = 0),
  alpha = .8
) +
geom_point(
  mapping=aes(color=condition),
  position = position_jitter(width = .15),
  size = .5,
  alpha = 0.8
) +
geom_boxplot(
  width = .1,
  outlier.shape = NA,
  alpha = 0.5
) +
scale_x_discrete(
  name="Condition",
  limits=condition_order
ylab("Extra traits final dominant") +
facet_wrap(
  ~extra_task_value,
  labeller=label_both
) +
theme(
  legend.position="none"
ggsave(
 pasteO(working_directory, "plots/dominant-extra-tasks.pdf"),
  width=15,
  height=10
)
```

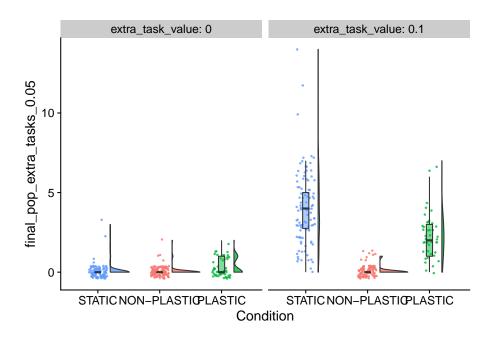


```
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
kruskal.test(
  formula=dominant_extra_tasks~condition,
  data=dom_task_data
##
##
    Kruskal-Wallis rank sum test
##
## data: dominant_extra_tasks by condition
## Kruskal-Wallis chi-squared = 177.17, df = 2, p-value < 2.2e-16
pairwise.wilcox.test(
  x=dom_task_data$dominant_extra_tasks,
  g=dom_task_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
  conf.level=0.95
)
```

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

##

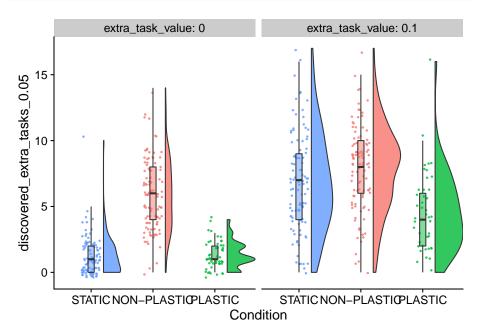
```
ggplot(summary_data, aes(x=condition, y=final_pop_extra_tasks_0.05, fill=condition)) +
  geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
  geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
 ) +
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order
 facet_wrap(
   ~extra_task_value,
   labeller=label both
 ) +
 theme(
   legend.position="none"
```



4.7 Population-level tasks discovered

```
ggplot(summary_data, aes(x=condition, y=discovered_extra_tasks_0.05, 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
  ) +
 facet_wrap(
```

```
"extra_task_value,
  labeller=label_both
) +
theme(
  legend.position="none"
)
```

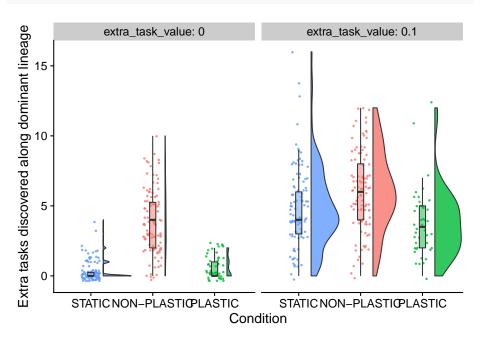


4.8 Extra tasks along lineage of final dominant genotype

4.8.1 Tasks discovered

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_discovered, fill=condition)
geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
) +
geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
) +
```

```
geom_boxplot(
  width = .1,
  outlier.shape = NA,
  alpha = 0.5
) +
scale_x_discrete(
  name="Condition",
  limits=condition_order
ylab("Extra tasks discovered along dominant lineage") +
facet_wrap(
  ~extra_task_value,
 labeller=label_both
) +
theme(
  legend.position="none"
ggsave(
  paste0(working_directory, "plots/dominant-lineage-extra-tasks-discovered.pdf"),
  width=15,
  height=10
)
```



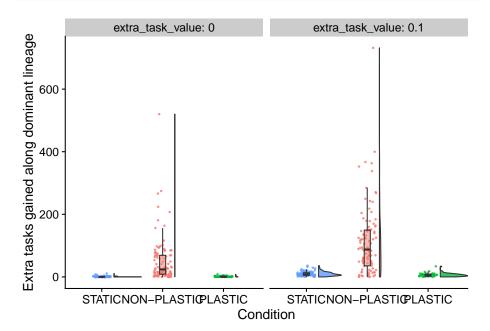
```
reward_level <- 0.1
dom_task_data <- filter(summary_data, extra_task_value==reward_level)</pre>
```

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

4.8.2 Tasks gained

```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_gained, fill=condition)) +
geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
) +
geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
) +
geom_boxplot(
   width = .1,
   outlier.shape = NA,
```

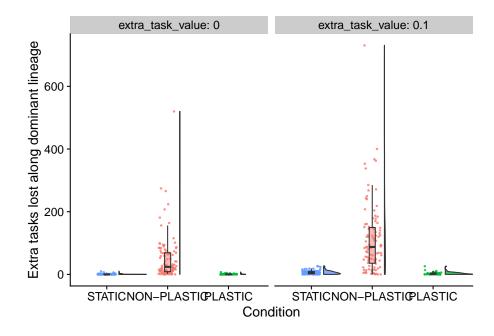
```
alpha = 0.5
) +
scale_x_discrete(
 name="Condition",
 limits=condition_order
ylab("Extra tasks gained along dominant lineage") +
facet_wrap(
  ~extra_task_value,
  labeller=label_both
theme(
  legend.position="none"
) +
ggsave(
  paste0(working_directory, "plots/dominant-lineage-extra-tasks-gained.pdf"),
  width=15,
  height=10
```



4.8.3 Tasks lost

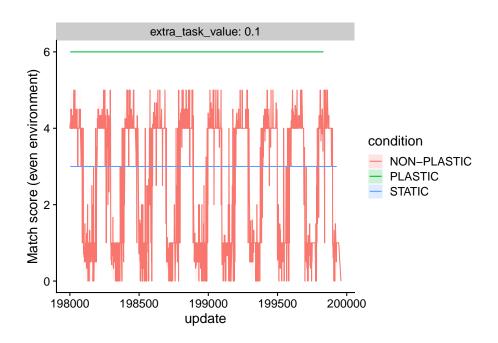
```
ggplot(summary_data, aes(x=condition, y=dominant_lineage_extra_traits_lost, fill=condit
geom_flat_violin(
```

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



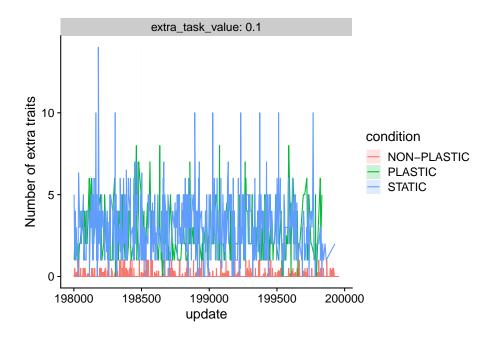
4.9 Extra task performance over time

```
Match score over time
lineage_reward10 <- filter(lineage_time_series_data, extra_task_value=="0.1")</pre>
ggplot(filter(lineage_reward10, update>198000 & update<=200000), aes(x=update, y=match</pre>
  stat_summary(fun="mean", geom="line") +
  stat_summary(
    fun.data="mean_cl_boot",
    fun.args=list(conf.int=0.95),
    geom="ribbon",
    alpha=0.2,
    linetype=0
  ) +
 ylab("Match score (even environment)") +
  facet_wrap(
    ~extra_task_value,
    labeller=label_both
  ) +
    paste0(working_directory, "plots/dominant-lineage-match-score-even-val10.png"),
    width=15,
    height=10
```



Extra tasks over time

```
ggplot(filter(lineage_reward10, update>198000 & update<=200000), aes(x=update, y=extra_traits, co</pre>
  stat_summary(fun="mean", geom="line") +
  stat_summary(
    fun.data="mean_cl_boot",
    fun.args=list(conf.int=0.95),
    geom="ribbon",
    alpha=0.2,
    linetype=0
  ) +
 ylab("Number of extra traits") +
 facet_wrap(
    ~extra_task_value,
    labeller=label_both
  ggsave(
    paste0(working_directory, "plots/dominant-lineage-extra-traits-val10.png"),
    width=15,
    height=10
```



4.10 Manuscript figures

Figures for the manuscript.

Final dominant extra tasks.

```
extra_task_reward_value=0.1
dominant_extra_tasks_fig <- ggplot(</pre>
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_extra_tasks, fill=condition)
 ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
```

```
) +
scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
) +
scale_y_continuous(
   name="Final dominant novel traits"
) +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
theme(
   legend.position="none"
) +
coord_flip()
```

Final dominant lineage tasks discovered.

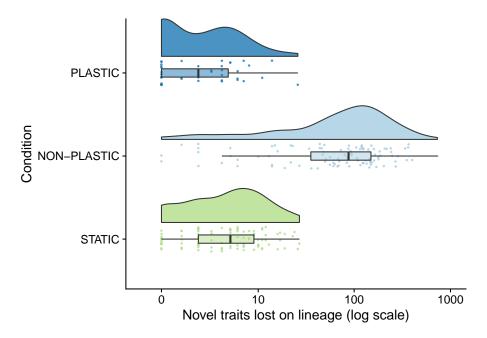
```
lineage_extra_tasks_discovered_fig <- ggplot(</pre>
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_lineage_extra_traits_discovered, fill=condition)
 ) +
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  ) +
  geom_point(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

```
scale_y_continuous(
   name="Novel traits discovered on lineage"
) +
scale_fill_brewer(
   palette="Paired"
) +
scale_color_brewer(
   palette="Paired"
) +
theme(
   legend.position="none"
) +
coord_flip()
```

Final dominant lineage tasks lost.

```
lineage_extra_tasks_lost_fig <- ggplot(</pre>
    filter(summary_data, extra_task_value==extra_task_reward_value),
    aes(x=condition, y=dominant_lineage_extra_traits_lost, fill=condition)
  geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
  geom point(
    mapping=aes(color=condition),
    position = position_jitter(width = .15),
    size = .5,
    alpha = 0.8
  ) +
  geom_boxplot(
    width = .1,
    outlier.shape = NA,
    alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
 ) +
  scale_y_continuous(
    name="Novel traits lost on lineage (log scale)",
    trans="pseudo_log",
    breaks=c(0,10,100,1000),
    limits=c(-1,1000)
```

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



Pull it all together.

```
grid <- plot_grid(
  dominant_extra_tasks_fig,
  lineage_extra_tasks_discovered_fig + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=element_blank(),axis.text.y=elem
```

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```
grid,
base_height=6,
base_asp=2.5
)
```

Chapter 5

The effect of phenotypic plasticity on neutral genetic hitchhiking

5.1 Overview

```
total_updates <- 200000
replicates <- 100

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

# Relative location of data.
working_directory <- "experiments/2021-01-31-neutral-hitchhiking/analysis/" # << For bookdown
# working_directory <- "./"</pre>
```

5.2 Analysis dependencies

Load all required R libraries.

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

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
                  0.3
                  2020
## year
## month
                 10
## day
                  10
                  79318
## svn rev
## language
                  R
## version.string R version 4.0.3 (2020-10-10)
## nickname
                  Bunny-Wunnies Freak Out
```

5.3 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_SENSO
summary_data$chg_env <- summary_data$chg_env == "True"</pre>
summary_data<mark>$</mark>dominant_plastic_odd_even <- <mark>as.factor</mark>(summary_data<mark>$</mark>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 {
```

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```
return("No sensors")
 }
}
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
  } else if (env_chg) {
    return("NON-PLASTIC")
 } else {
    return("STATIC")
 }
}
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
summary_data$condition <- mapply(</pre>
  condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
)
condition order = c(
  "STATIC",
 "NON-PLASTIC",
  "PLASTIC"
)
##### time series #####
lineage_time_series_data_loc <- paste0(working_directory, "data/lineage_series.csv")</pre>
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_data$DISABLE_I
lineage_time_series_data$chg_env <- lineage_time_series_data$chg_env == "True"
lineage_time_series_data$sensors <- lineage_time_series_data$DISABLE_REACTION_SENSORS == "0"
lineage_time_series_data$env_label <- mapply(</pre>
  env_label_fun,
  lineage_time_series_data$chg_env
```

```
lineage_time_series_data$sensors_label <- mapply(
    sensors_label_fun,
    lineage_time_series_data$sensors
)
lineage_time_series_data$condition <- mapply(
    condition_label_fun,
    lineage_time_series_data$sensors,
    lineage_time_series_data$sensors,
    lineage_time_series_data$chg_env
)

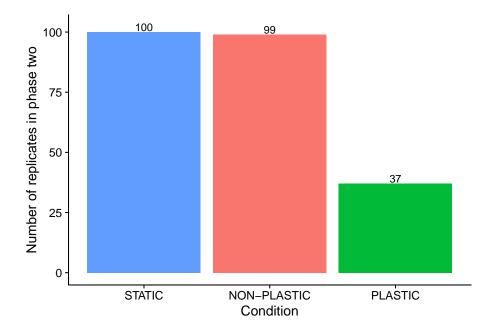
####### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)</pre>
```

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)
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
) +
    ylab("Number of replicates in phase two") +
    theme(
        legend.position="none"
)
```

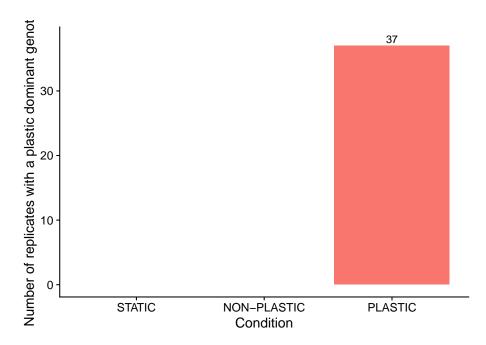


One NON-PLASTIC population went extinct early in phase 2.

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())
```

```
## `summarise()` has grouped output by 'condition'. You can override using the `.groups` argument
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    geom_text(aes(label=n, y=n+1)) +
    ylab("Number of replicates with a plastic dominant genotype") +
    theme(
        legend.position="none")
```

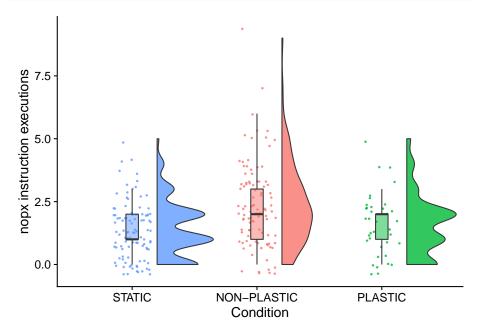


5.5 Hitchhiking instruction execution

5.5.1 Final dominant genotype

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

```
ylab("nopx instruction executions") +
theme(
  legend.position="none"
) +
ggsave(
  paste0(working_directory, "plots/dominant-nopx.pdf"),
  width=15,
  height=10
)
```



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

##

## Kruskal-Wallis rank sum test

##

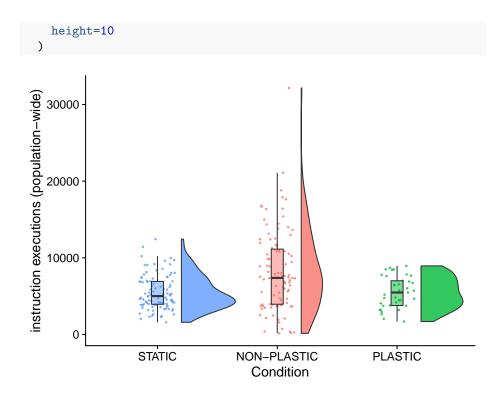
## data: dominant_times_nopx_executed by condition

## Kruskal-Wallis chi-squared = 20.931, df = 2, p-value = 2.85e-05

pairwise.wilcox.test(
  x=summary_data$dominant_times_nopx_executed,
  g=summary_data$condition,
  p.adjust.method="bonferroni",
  conf.int=TRUE,
```

5.5.2 Final population

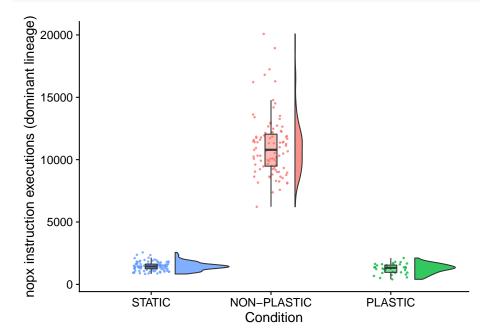
```
ggplot(summary_data, aes(x=condition, y=final_population_nopx, fill=condition)) +
 geom_flat_violin(
   position = position_nudge(x = .2, y = 0),
   alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  ) +
 geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ) +
 scale_y_continuous(
   name="instruction executions (population-wide)"
 ) +
 theme(
   legend.position="none"
 ggsave(
   pasteO(working_directory, "plots/final-population-nopx.pdf"),
   width=15,
```



5.6 Final dominant lineage (cumulative)

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

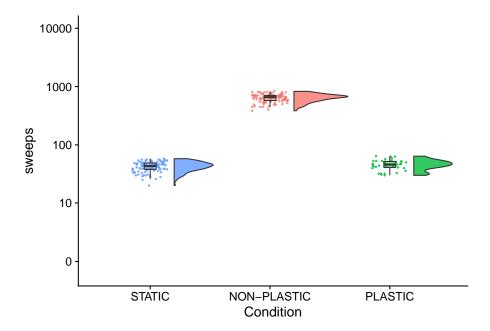
```
limits=condition_order
) +
scale_y_continuous(
  name="nopx instruction executions (dominant lineage)"
) +
theme(
  legend.position="none"
) +
ggsave(
  paste0(working_directory, "plots/final-dominant-lineage-nopx.pdf"),
  width=15,
  height=10
)
```



5.7 MRCA Changes

```
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_x_discrete(
 name="Condition",
  limits=condition_order
) +
scale_y_continuous(
name="sweeps",
 trans="pseudo_log",
 breaks=c(0,10,100,1000,10000),
  limits=c(-1,10000)
) +
theme(
  legend.position="none"
) +
  pasteO(working_directory, "plots/selective-sweeps.pdf"),
  width=15,
  height=10
)
```

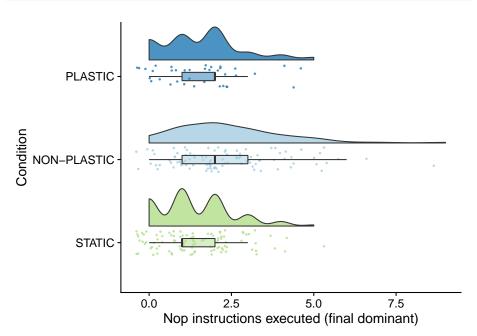


5.8 Manuscript figures

Final dominant nop-x execution.

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

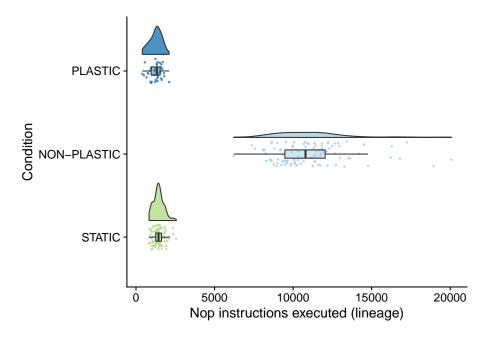
```
name="Condition",
   limits=condition_order,
   labels=condition_order
  ) +
  scale_y_continuous(
   name="Nop instructions executed (final dominant)"
  scale_fill_brewer(
   palette="Paired"
 ) +
  scale_color_brewer(
   palette="Paired"
  ) +
  theme(
   legend.position="none"
  ) +
  coord_flip()
dominant_inst_exec
```



Lineage (cumulative).

```
lineage_inst_exec <- ggplot(
    summary_data,
    aes(x=condition, y=dominant_lineage_times_nopx_executed, fill=condition)
) +</pre>
```

```
geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
   alpha = .8
  ) +
  geom_point(
    mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
  ) +
  scale_x_discrete(
   name="Condition",
   limits=condition_order,
   labels=condition_order
  ) +
  scale_y_continuous(
   name="Nop instructions executed (lineage)"
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  theme(
   legend.position="none"
  ) +
  coord_flip()
lineage_inst_exec
```



Pull it all together.

```
grid <- plot_grid(
  dominant_inst_exec,
  lineage_inst_exec + theme(axis.ticks.y=element_blank(),axis.text.y=element_blank(),axis.title.y
  nrow=1,
  align="v",
  labels="auto"
)
save_plot(
  pasteO(working_directory, "plots/", "neutral-hitchhiking-panel.pdf"),
  grid,
  base_height=6,
  base_asp=2.5</pre>
```

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Chapter 6

The effect of phenotypic plasticity on deleterious genetic hitchhiking

6.1 Overview

```
total_updates <- 2000000
replicates <- 100

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

# Relative location of data.
working_directory <- "experiments/2021-01-31-deleterious-hitchhiking/analysis/" # << For bookdown
# working_directory <- "./"</pre>
```

6.2 Analysis dependencies

Load all required R libraries.

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

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
                  0.3
                  2020
## year
## month
                 10
## day
                 10
                  79318
## svn rev
## language
                  R
## version.string R version 4.0.3 (2020-10-10)
## nickname
                  Bunny-Wunnies Freak Out
```

6.3 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)
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"
summary_data$POISON_PENALTY <- as.factor(summary_data$POISON_PENALTY)</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")
```

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```
} else {
    return("No sensors")
}
condition_label_fun <- function(has_sensors, env_chg) {</pre>
  if (has_sensors && env_chg) {
    return("PLASTIC")
  } else if (env_chg) {
    return("NON-PLASTIC")
  } else {
    return("STATIC")
 }
summary_data$env_label <- mapply(</pre>
  env_label_fun,
  summary_data$chg_env
summary_data$sensors_label <- mapply(</pre>
  sensors_label_fun,
  summary_data$sensors
summary_data$condition <- mapply(</pre>
  condition_label_fun,
  summary_data$sensors,
  summary_data$chg_env
condition_order = c(
 "STATIC",
  "NON-PLASTIC",
  "PLASTIC"
)
###### time series #####
lineage_time_series_data_loc <- paste0(working_directory, "data/lineage_series.csv")</pre>
lineage_time_series_data <- read.csv(lineage_time_series_data_loc)</pre>
lineage_time_series_data$DISABLE_REACTION_SENSORS <- as.factor(lineage_time_series_data$DISABLE_I
lineage_time_series_data$chg_env <- lineage_time_series_data$chg_env == "True"
lineage_time_series_data$sensors <- lineage_time_series_data$DISABLE_REACTION_SENSORS == "0"
lineage_time_series_data$POISON_PENALTY <- as.factor(lineage_time_series_data$POISON_VALUE)
lineage_time_series_data$env_label <- mapply(</pre>
```

```
env_label_fun,
  lineage_time_series_data$chg_env
)
lineage_time_series_data$sensors_label <- mapply(
  sensors_label_fun,
  lineage_time_series_data$sensors
)
lineage_time_series_data$condition <- mapply(
  condition_label_fun,
  lineage_time_series_data$sensors,
  lineage_time_series_data$sensors,
  lineage_time_series_data$chg_env
)

####### misc ######
# Configure our default graphing theme
theme_set(theme_cowplot())
dir.create(paste0(working_directory, "plots"), showWarnings=FALSE)</pre>
```

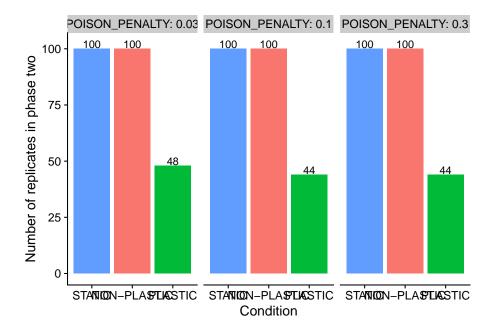
6.4 Evolution of phenotypic plasticity

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

```
summary_data_group_counts = dplyr::summarize(summary_data_grouped, n=dplyr::n())
## `summarise()` has grouped output by 'sensors', 'env_label', 'condition'. You can ove
ggplot(summary_data_group_counts, aes(x=condition, y=n, fill=condition)) +
```

summary_data_grouped = dplyr::group_by(summary_data, sensors, env_label, condition, PO

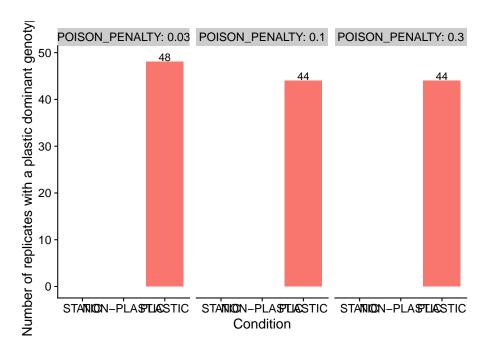
```
ggplot(summary_data_group_counts, aes(x=condition, y=n, lill=condit
geom_col(position=position_dodge(0.9)) +
geom_text(aes(label=n, y=n+2)) +
scale_x_discrete(
    name="Condition",
    limits=condition_order
) +
ylab("Number of replicates in phase two") +
facet_wrap(~POISON_PENALTY, labeller=label_both) +
theme(
    legend.position="none"
)
```



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

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

```
## `summarise()` has grouped output by 'condition', 'is_plastic'. You can override using the `.gr
ggplot(filter(summary_data_group_counts, is_plastic), aes(x=condition, y=n, fill=condition)) +
    geom_col(position=position_dodge(0.9)) +
    scale_x_discrete(
        name="Condition",
        limits=condition_order
) +
    geom_text(aes(label=n, y=n+1)) +
    ylab("Number of replicates with a plastic dominant genotype") +
    facet_wrap(~POISON_PENALTY, labeller=label_both) +
    theme(
    legend.position="none"
```

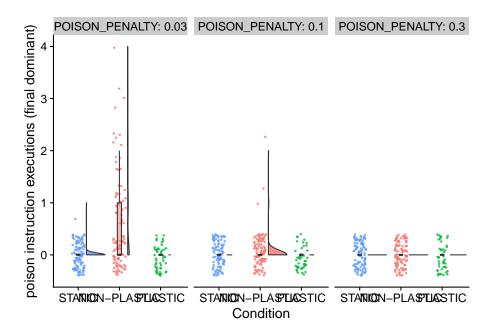


6.5 Hitchhiking instruction execution

6.5.1 Final dominant genotype

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

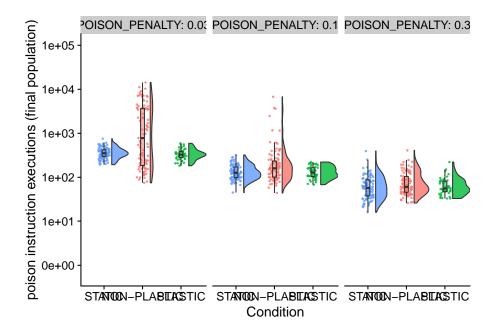
```
ylab("poison instruction executions (final dominant)") +
facet_wrap(
   ~POISON_PENALTY,
   labeller=label_both
) +
theme(
   legend.position="none"
) +
ggsave(
   paste0(working_directory, "plots/dominant-poison.pdf"),
   width=15,
   height=10
)
```



```
# threshold <- 0.03
# dom_data <- filter(summary_data, POISON_PENALTY==threshold)
# kruskal.test(
# formula=dominant_times_poison_executed~condition,
# data=dom_data
# )</pre>
```

6.5.2 Final population

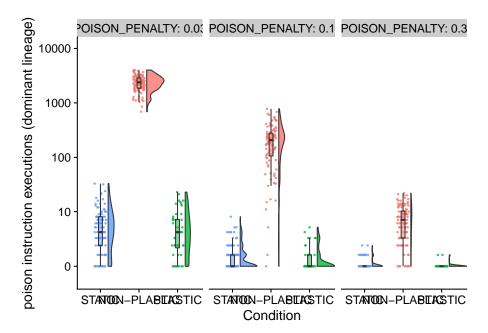
```
ggplot(summary_data, aes(x=condition, y=final_population_poison, fill=condition)) +
 geom_flat_violin(
    position = position_nudge(x = .2, y = 0),
    alpha = .8
 ) +
 geom_point(
   mapping=aes(color=condition),
   position = position_jitter(width = .15),
   size = .5,
   alpha = 0.8
  geom_boxplot(
   width = .1,
   outlier.shape = NA,
   alpha = 0.5
 ) +
 scale_x_discrete(
   name="Condition",
   limits=condition_order
 ) +
  scale_y_continuous(
    name="poison instruction executions (final population)",
    trans="pseudo_log",
    breaks=c(0,10,100,1000, 10000, 100000),
   limits=c(-1,100000)
 facet_wrap(
    ~POISON_PENALTY,
   labeller=label both
 ) +
 theme(
    legend.position="none"
  ggsave(
   pasteO(working_directory, "plots/final-population-poison-log.pdf"),
   width=15,
   height=10
 )
```



6.6 Final dominant lineage (cumulative)

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

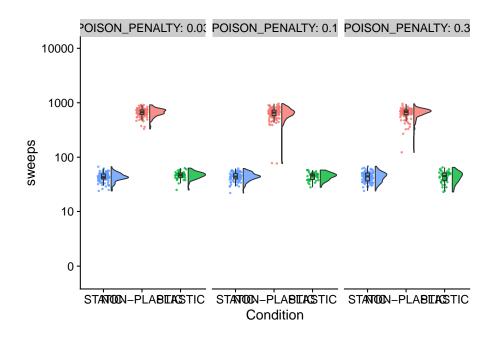
```
name="poison instruction executions (dominant lineage)",
  trans="pseudo_log",
  breaks=c(0,10,100,1000, 10000),
  limits=c(-1,10000)
) +
facet_wrap(
  ~POISON_PENALTY,
  labeller=label_both
) +
theme(
  legend.position="none"
ggsave(
  paste0(working_directory, "plots/final-dominant-lineage-poison-log.pdf"),
  width=15,
  height=10
)
```



6.7 MRCA Changes

```
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_x_discrete(
  name="Condition",
  limits=condition_order
scale_y_continuous(
 name="sweeps",
  trans="pseudo_log",
  breaks=c(0,10,100,1000,10000),
  limits=c(-1,10000)
) +
facet_wrap(
  ~POISON_PENALTY,
  labeller=label_both
) +
theme(
  legend.position="none"
) +
ggsave(
  pasteO(working_directory, "plots/selective-sweeps.pdf"),
  width=15,
  height=10
```

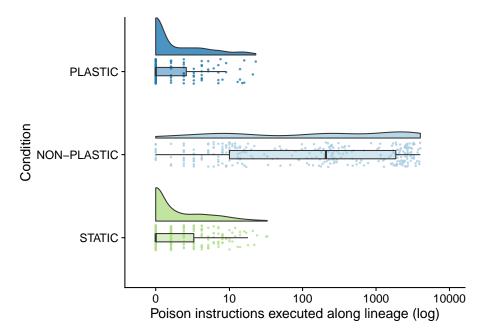


6.8 Manuscript figures

Lineage (cumulative)

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

```
name="Condition",
   limits=condition_order,
   labels=condition_order
  ) +
  scale_y_continuous(
   name="Poison instructions executed along lineage (log)",
   trans="pseudo_log",
   breaks=c(0,10,100,1000, 10000),
   limits=c(-1,10000)
 ) +
  scale_fill_brewer(
   palette="Paired"
  scale_color_brewer(
   palette="Paired"
  ) +
  theme(
   legend.position="none"
  coord_flip()
lineage_inst_exec
```



```
lineage_inst_exec +
ggsave(
   paste0(working_directory, "plots/", "deleterious-hitchhiking-panel.pdf"),
```

