

Data analyses for Experiment 1

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This code analyzes the data associated with Experiment 1 and produces Figure 2 in the manuscript:

Barnes DK, Burgess SC. Fitness consequences of marine larval dispersal: the role of neighborhood density, spatial arrangement, and genetic relatedness on survival, growth, reproduction, and paternity. *Journal of Evolutionary Biology*

Code finalized September 2024.

Any comments or error reporting, please contact Scott Burgess: sburgess@bio.fsu.edu

Load required libraries

```
library('tidyverse')
library('glmmTMB')
library('gridExtra')
```

```
sessionInfo()
```

```
## R version 4.4.0 (2024-04-24)
## Platform: aarch64-apple-darwin20
## Running under: macOS Sonoma 14.6.1
##
## Matrix products: default
## BLAS:   /Library/Frameworks/R.framework/Versions/4.4-arm64/Resources/lib/libRblas.0.dylib
## LAPACK: /Library/Frameworks/R.framework/Versions/4.4-arm64/Resources/lib/libRlapack.dylib; LAPACK v
##
## locale:
## [1] en_US.UTF-8/en_US.UTF-8/en_US.UTF-8/C/en_US.UTF-8/en_US.UTF-8
##
## time zone: America/New_York
## tzcode source: internal
##
## attached base packages:
## [1] stats      graphics  grDevices  utils      datasets  methods   base
##
## other attached packages:
## [1] gridExtra_2.3   glmmTMB_1.1.9   lubridate_1.9.3 forcats_1.0.0
## [5] stringr_1.5.1   dplyr_1.1.4     purrr_1.0.2     readr_2.1.5
## [9] tidyr_1.3.1     tibble_3.2.1    ggplot2_3.5.1   tidyverse_2.0.0
##
## loaded via a namespace (and not attached):
## [1] utf8_1.2.4      generics_0.1.3   stringi_1.8.4
## [4] lattice_0.22-6  lme4_1.1-35.3    hms_1.1.3
## [7] digest_0.6.35   magrittr_2.0.3   estimability_1.5.1
```

```
## [10] evaluate_0.23      grid_4.4.0          timechange_0.3.0
## [13] mvtnorm_1.2-5      fastmap_1.2.0       Matrix_1.7-0
## [16] mgcv_1.9-1         fansi_1.0.6         scales_1.3.0
## [19] numDeriv_2016.8-1.1 cli_3.6.2           rlang_1.1.3
## [22] munsell_0.5.1      splines_4.4.0       withr_3.0.0
## [25] yaml_2.3.8         tools_4.4.0         tzdb_0.4.0
## [28] coda_0.19-4.1      nloptr_2.0.3        minqa_1.2.7
## [31] colorspace_2.1-0   boot_1.3-30         vctrs_0.6.5
## [34] R6_2.5.1           emmeans_1.10.2      lifecycle_1.0.4
## [37] MASS_7.3-60.2      pkgconfig_2.0.3     pillar_1.9.0
## [40] gtable_0.3.5       Rcpp_1.0.12         glue_1.7.0
## [43] xfun_0.44          tidyselect_1.2.1    rstudioapi_0.16.0
## [46] knitr_1.47         xtable_1.8-4        htmltools_0.5.8.1
## [49] nlme_3.1-164       rmarkdown_2.28      TMB_1.9.11
## [52] compiler_4.4.0
```

Import data for Experiment 1

```
dat <- read.csv("Data/Experiment_1.csv")
```

Create a vector of the ages at which data were recorded. Note that individuals were reared in the lab for 17 days, so age 25 days is 8 days in the field, and age 32 days is 15 days in the field

```
Age.days.vec <- unique(dat$Age.days)
Age.days.vec
```

```
## [1] 17 25 32
```

Survival

Fit generalized linear mixed effects model with a binomial distribution and random effect of plate number (Unique.ID).

Survival after 8 days in the field

```
d <- dat %>% filter(Age.days == Age.days.vec[2])

survival1 <- glmmTMB(Survival ~ Density * Relatedness +
  (1|Unique.ID),
  family = "binomial",
  data = d)

survival2 <- glmmTMB(Survival ~ Density + Relatedness +
  (1|Unique.ID),
  family = "binomial",
  data = d)

survival3 <- glmmTMB(Survival ~ Density +
  (1|Unique.ID),
  family = "binomial",
  data = d)

survival4 <- glmmTMB(Survival ~ Relatedness +
  (1|Unique.ID),
```

```
family = "binomial",
data = d)
```

Test the interaction

```
result1 <- round(anova(survival1, survival2, test="Chisq"), 3)
result1
```

```
## Data: d
## Models:
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## survival1: Survival ~ Density * Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival2  4 245.28 258.35 -118.64  237.28
## survival1  5 247.06 263.39 -118.53  237.06 0.225      1      0.636
```

Test relatedness

```
result2 <- round(anova(survival2, survival3, test="Chisq"), 3)
result2
```

```
## Data: d
## Models:
## survival3: Survival ~ Density + (1 | Unique.ID), zi=~0, disp=~1
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival3  3 244.91 254.71 -119.45  238.91
## survival2  4 245.28 258.35 -118.64  237.28 1.626      1      0.202
```

Test density

```
result3 <- round(anova(survival2, survival4, test="Chisq"), 3)
result3
```

```
## Data: d
## Models:
## survival4: Survival ~ Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival4  3 253.55 263.35 -123.77  247.55
## survival2  4 245.28 258.35 -118.64  237.28 10.268      1      0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
odds.effect <- round((1 - exp(confint(survival2)[2,])) * 100, 2)
```

Results text:

The probability of individual colony survival in the field declined with density after 8 days ($\chi^2 = 10.268$, df = 1, p = 0.001).

The odds of survival declined by 10.07 (4.03 - 15.72) for every additional neighbor colony.

There was no evidence that relatedness had additive ($\chi^2 = 1.626$, df = 1, p = 0.202) or interactive effects ($\chi^2 = 0.225$, df = 1, p = 0.636) on survival.

Calculate fitted values for plotting

```
predictions_survival_8days <- expand.grid(
  Density = seq(0, 20, 0.1),
```

```

    Relatedness = unique(dat$Relatedness))

p <- predict(survival2,
             predictions_survival_8days,
             type = "link",
             se.fit = T,
             re.form = NA)

predictions_survival_8days$fit <- plogis(p$fit)
predictions_survival_8days$se.fit <- p$se.fit
# Calculate confidence intervals
predictions_survival_8days$lwr <- plogis(p$fit - 2 * p$se.fit)
predictions_survival_8days$upr <- plogis(p$fit + 2 * p$se.fit)

```

Survival after 15 days in the field

```

d <- dat %>% filter(Age.days == Age.days.vec[3])

survival1 <- glmmTMB(Survival ~ Density * Relatedness +
                    (1|Unique.ID),
                    family = "binomial",
                    data = d)

survival2 <- glmmTMB(Survival ~ Density + Relatedness +
                    (1|Unique.ID),
                    family = "binomial",
                    data = d)

survival3 <- glmmTMB(Survival ~ Density +
                    (1|Unique.ID),
                    family = "binomial",
                    data = d)

survival4 <- glmmTMB(Survival ~ Relatedness +
                    (1|Unique.ID),
                    family = "binomial",
                    data = d)

```

Test the interaction

```

result1 <- round(anova(survival1, survival2, test="Chisq"), 3)
result1

```

```

## Data: d
## Models:
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## survival1: Survival ~ Density * Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df    AIC    BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival2  4 262.71 275.78 -127.36  254.71
## survival1  5 262.16 278.50 -126.08  252.16 2.551    1    0.11

```

Test relatedness

```

result2 <- round(anova(survival2, survival3, test="Chisq"), 3)
result2

```

```
## Data: d
## Models:
## survival3: Survival ~ Density + (1 | Unique.ID), zi=~0, disp=~1
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival3  3 263.07 272.88 -128.54  257.07
## survival2  4 262.71 275.78 -127.36  254.71 2.363      1      0.124
```

Test density

```
result3 <- round(anova(survival2, survival4, test="Chisq"), 3)
result3
```

```
## Data: d
## Models:
## survival4: Survival ~ Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## survival2: Survival ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## survival4  3 269.06 278.86 -131.53  263.06
## survival2  4 262.71 275.78 -127.36  254.71 8.346      1      0.004 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
odds.effect <- round((1 - exp(confint(survival2)[2,])) * 100, 2)
```

Results text:

The probability of individual colony survival in the field declined with density after 15 days ($\chi^2 = 8.346$, df = 1, p = 0.004).

The odds of survival declined by 8.46 (2.9 - 13.71) for every additional neighbor colony.

There was no evidence that relatedness had additive ($\chi^2 = 2.363$, df = 1, p = 0.124) or interactive effects ($\chi^2 = 2.551$, df = 1, p = 0.11) on survival.

Calculate fitted values for plotting

```
predictions_survival_15days <- expand.grid(
  Density = seq(0, 20, 0.1),
  Relatedness = unique(dat$Relatedness))

p <- predict(survival2,
  predictions_survival_15days,
  type = "link",
  se.fit = T,
  re.form = NA)

predictions_survival_15days$fit <- plogis(p$fit)
predictions_survival_15days$se.fit <- p$se.fit
# Calculate confidence intervals
predictions_survival_15days$lwr <- plogis(p$fit - 2 * p$se.fit)
predictions_survival_15days$upr <- plogis(p$fit + 2 * p$se.fit)
```

Relative growth rate

Change data to the wide format

```
dat_wide <- dat %>% pivot_wider(id_cols = Unique.ID:Inside.outside,  
                                names_from = Age.days,  
                                values_from = c(Survival, Bifurcations,Zooids))
```

Calculate relative growth rate

8 days

```
dat_wide$relgrowth.collection1 <- (log(dat_wide$Zooids_25)- log(dat_wide$Zooids_17)) / (25-17)
```

15 days

```
dat_wide$relgrowth.collection2 <- (log(dat_wide$Zooids_32)- log(dat_wide$Zooids_17)) / (32-17)
```

Fit generalized linear mixed effects model with a Gaussian distribution and random effect of plate number (Unique.ID).

Relative growth rate after 8 days in the field

```
rgr1 <- glmmTMB(relgrowth.collection1 ~ Density * Relatedness +  
               (1|Unique.ID),  
               data = dat_wide,  
               family = gaussian())  
  
rgr2 <- glmmTMB(relgrowth.collection1 ~ Density + Relatedness +  
               (1|Unique.ID),  
               data = dat_wide,  
               family = gaussian())  
  
rgr3 <- glmmTMB(relgrowth.collection1 ~ Density +  
               (1|Unique.ID),  
               data = dat_wide,  
               family = gaussian())  
  
rgr4 <- glmmTMB(relgrowth.collection1 ~ Relatedness +  
               (1|Unique.ID),  
               data = dat_wide,  
               family = gaussian())
```

Test the interaction

```
result1 <- round(anova(rgr1, rgr2,test="Chisq"), 3)  
result1
```

```
## Data: dat_wide  
## Models:  
## rgr2: relgrowth.collection1 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1  
## rgr1: relgrowth.collection1 ~ Density * Relatedness + (1 | Unique.ID), zi=~0, disp=~1  
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)  
## rgr2  5 -251.39 -237.33 130.69 -261.39
```

```
## rgr1  6 -249.45 -232.58 130.73 -261.45 0.065      1      0.799
```

Test relatedness

```
result2 <- round(anova(rgr2, rgr3, test="Chisq"), 3)
result2
```

```
## Data: dat_wide
```

```
## Models:
```

```
## rgr3: relgrowth.collection1 ~ Density + (1 | Unique.ID), zi=~0, disp=~1
```

```
## rgr2: relgrowth.collection1 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
```

```
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
```

```
## rgr3  4 -253.09 -241.84 130.55 -261.09
```

```
## rgr2  5 -251.39 -237.33 130.69 -261.39 0.295      1      0.587
```

Test density

```
result3 <- round(anova(rgr2, rgr4, test="Chisq"), 3)
result3
```

```
## Data: dat_wide
```

```
## Models:
```

```
## rgr4: relgrowth.collection1 ~ Relatedness + (1 | Unique.ID), zi=~0, disp=~1
```

```
## rgr2: relgrowth.collection1 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
```

```
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
```

```
## rgr4  4 -252.35 -241.10 130.18 -260.35
```

```
## rgr2  5 -251.39 -237.33 130.69 -261.39 1.034      1      0.309
```

Results text:

No evidence that density ($\chi^2 = 1.034$, $df = 1$, $p = 0.309$) or relatedness ($\chi^2 = 0.295$, $df = 1$, $p = 0.587$) had additive or interactive effects ($\chi^2 = 0.065$, $df = 1$, $p = 0.799$) on relative growth rate.

Calculate fitted values for plotting

```
predictions_rgr_8days <- expand.grid(
  Density = seq(0, 20, 0.1),
  Relatedness = unique(dat$Relatedness))

p <- predict(rgr2,
  predictions_rgr_8days,
  type = "link",
  se.fit = T,
  re.form = NA)

predictions_rgr_8days$fit <- p$fit
predictions_rgr_8days$se.fit <- p$se.fit
# Calculate confidence intervals
predictions_rgr_8days$lower <- p$fit - 2 * p$se.fit
predictions_rgr_8days$upper <- p$fit + 2 * p$se.fit
```

Relative growth rate after 15 days in the field

```
rgr1 <- glmmTMB(relgrowth.collection2 ~ Density * Relatedness +
  (1|Unique.ID),
  data = dat_wide,
  family = gaussian())
```

```

rgr2 <- glmmTMB(relgrowth.collection2 ~ Density + Relatedness +
  (1|Unique.ID),
  data = dat_wide,
  family = gaussian())

rgr3 <- glmmTMB(relgrowth.collection2 ~ Density +
  (1|Unique.ID),
  data = dat_wide,
  family = gaussian())

rgr4 <- glmmTMB(relgrowth.collection2 ~ Relatedness +
  (1|Unique.ID),
  data = dat_wide,
  family = gaussian())

```

Test the interaction

```

result1 <- round(anova(rgr1, rgr2, test="Chisq"), 3)
result1

```

```

## Data: dat_wide
## Models:
## rgr2: relgrowth.collection2 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## rgr1: relgrowth.collection2 ~ Density * Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## rgr2  5 -298.12 -285.1 154.06  -308.12
## rgr1  6 -298.43 -282.8 155.21  -310.43 2.305      1      0.129

```

Test relatedness

```

result2 <- round(anova(rgr2, rgr3, test="Chisq"), 3)
result2

```

```

## Data: dat_wide
## Models:
## rgr3: relgrowth.collection2 ~ Density + (1 | Unique.ID), zi=~0, disp=~1
## rgr2: relgrowth.collection2 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## rgr3  4 -299.98 -289.56 153.99  -307.98
## rgr2  5 -298.12 -285.10 154.06  -308.12 0.142      1      0.706

```

Test density

```

result3 <- round(anova(rgr2, rgr4, test="Chisq"), 3)
result3

```

```

## Data: dat_wide
## Models:
## rgr4: relgrowth.collection2 ~ Relatedness + (1 | Unique.ID), zi=~0, disp=~1
## rgr2: relgrowth.collection2 ~ Density + Relatedness + (1 | Unique.ID), zi=~0, disp=~1
##      Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## rgr4  4 -297.74 -287.32 152.87  -305.74
## rgr2  5 -298.12 -285.10 154.06  -308.12 2.383      1      0.123

```

Results text: No evidence that density ($\chi^2 = 2.383$, $df = 1$, $p = 0.123$) or relatedness ($\chi^2 = 0.142$, $df = 1$, $p = 0.706$) had additive or interactive effects ($\chi^2 = 2.305$, $df = 1$, $p = 0.129$) on relative growth rate.

Calculate fitted values for plotting

```
predictions_rgr_15days <- expand.grid(
  Density = seq(0, 20, 0.1),
  Relatedness = unique(dat$Relatedness))

p <- predict(rgr2,
  predictions_rgr_15days,
  type = "link",
  se.fit = T,
  re.form = NA)

predictions_rgr_15days$fit <- p$fit
predictions_rgr_15days$se.fit <- p$se.fit
# Calculate confidence intervals
predictions_rgr_15days$lwr <- p$fit - 2 * p$se.fit
predictions_rgr_15days$upr <- p$fit + 2 * p$se.fit
```

Make Figure 2

```
my_colors <- c("#98c1d9", "#ee6c4d")
legend.labs <- c("Unrelated", "Siblings")

panel_A <- ggplot(data = predictions_survival_8days,
  aes(x = Density,
    y = fit,
    group = Relatedness)) +
  geom_ribbon(aes(ymin = lwr,
    ymax = upr,
    fill = Relatedness),
    alpha = 0.4) +
  geom_line(aes(color = Relatedness)) +
  scale_color_manual(values = my_colors,
    labels = legend.labs) +
  scale_fill_manual(values = my_colors,
    labels = legend.labs) +
  ylim(0,1) +
  labs(x = expression(paste("Density (colonies per 12", cm^2, ")")),
    y = "Probability of survival",
    title = "a) 8 days in the field") +
  theme_classic() +
  theme(legend.position = c(0.3, 0.25),
    legend.title=element_blank(),
    legend.background = element_rect(fill='transparent'))
```

```
## Warning: A numeric `legend.position` argument in `theme()` was deprecated in ggplot2
## 3.5.0.
## i Please use the `legend.position.inside` argument of `theme()` instead.
## This warning is displayed once every 8 hours.
## Call `lifecycle::last_lifecycle_warnings()` to see where this warning was
## generated.
```

```

panel_B <- ggplot(data = predictions_survival_15days,
  aes(x = Density,
      y = fit,
      group = Relatedness)) +
  geom_ribbon(aes(ymin = lwr,
                ymax = upr,
                fill = Relatedness),
            alpha = 0.4) +
  geom_line(aes(color = Relatedness)) +
  scale_color_manual(values = my_colors,
                    labels = legend.labs) +
  scale_fill_manual(values = my_colors,
                   labels = legend.labs) +
  ylim(0,1) +
  labs(x = expression(paste("Density (colonies per 12", cm^2, ")")),
       y = "Probability of survival",
       title = "b) 15 days in the field") +
  theme_classic() +
  theme(legend.position = c(0.3, 0.25),
        legend.title=element_blank(),
        legend.background = element_rect(fill='transparent'))

panel_C <- ggplot(data = predictions_rgr_8days,
  aes(x = Density,
      y = fit,
      group = Relatedness)) +
  geom_ribbon(aes(ymin = lwr,
                ymax = upr,
                fill = Relatedness),
            alpha = 0.4) +
  geom_line(aes(color = Relatedness)) +
  scale_color_manual(values = my_colors,
                    labels = legend.labs) +
  scale_fill_manual(values = my_colors,
                   labels = legend.labs) +
  ylim(0,0.25) +
  labs(x = expression(paste("Density (colonies per 12", cm^2, ")")),
       y = "Relative growth rate",
       title = "c) 8 days in the field") +
  theme_classic() +
  theme(legend.position = c(0.3, 0.25),
        legend.title=element_blank(),
        legend.background = element_rect(fill='transparent'))

panel_D <- ggplot(data = predictions_rgr_15days,
  aes(x = Density,
      y = fit,
      group = Relatedness)) +
  geom_ribbon(aes(ymin = lwr,
                ymax = upr,
                fill = Relatedness),
            alpha = 0.4) +

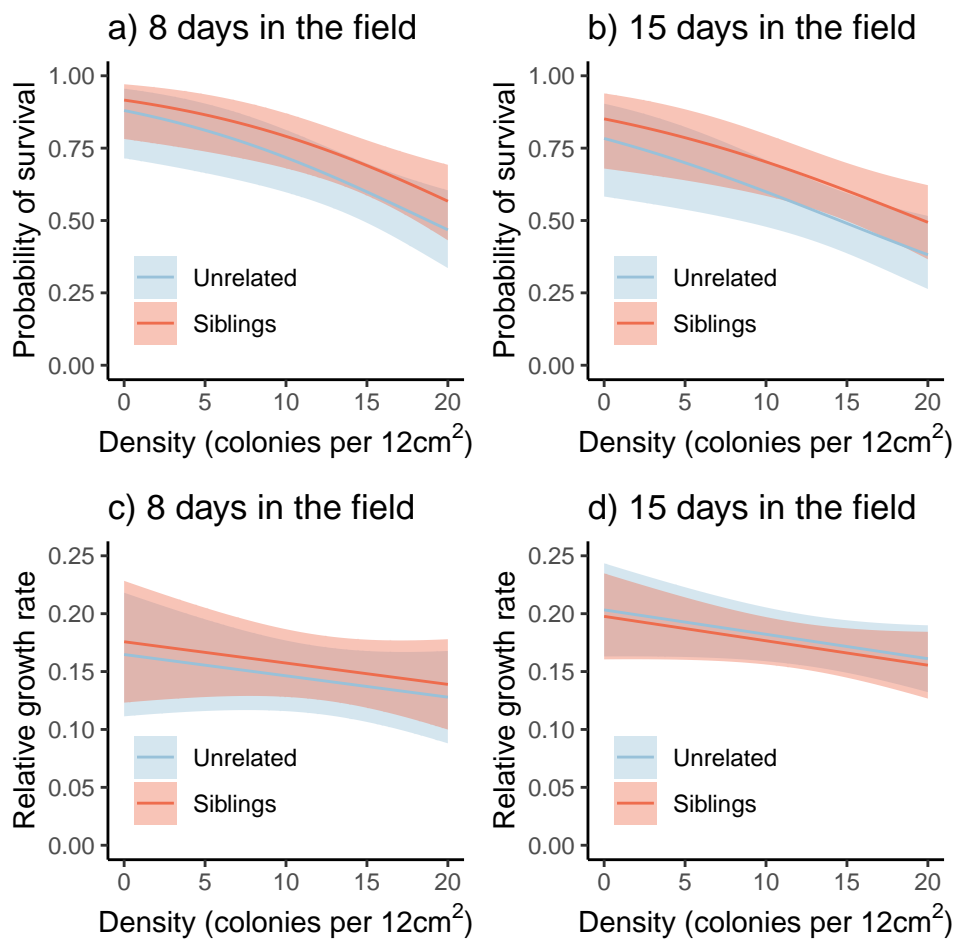
```

```

geom_line(aes(color = Relatedness)) +
scale_color_manual(values = my_colors,
                  labels = legend.labs) +
scale_fill_manual(values = my_colors,
                 labels = legend.labs) +
ylim(0,0.25) +
labs(x = expression(paste("Density (colonies per 12", cm^2, ")")),
     y = "Relative growth rate",
     title = "d) 15 days in the field") +
theme_classic() +
theme(legend.position = c(0.3, 0.25),
      legend.title=element_blank(),
      legend.background = element_rect(fill='transparent'))

grid.arrange(panel_A, panel_B, panel_C, panel_D,
             nrow = 2,
             ncol = 2)

```



```

## pdf
## 2

```