

Lathyrus ms3: Selective agents

Contents

```
# Load previously saved large objects
load("output/b_par_1.RData")
load("output/b_par_2.RData")
```

Data preparation

Load data, keep variables needed and merge

```
data_selag<-read.table("C:/Users/user/Dropbox/SU/Projects/lathyrus/lathyrus_ms1/data/clean/alldata_weathl
mean_weather<-read.table("C:/Users/user/Dropbox/SU/Projects/lathyrus/lathyrus_ms1/data/clean/mean_weathl
```

```
data_selag<-data_selag[c(1:7,9:10,12,14:15,17:18,21,22)]
data_selag$n_fl<-data_selag$cum_n_fl
data_selag$cum_n_fl<-NULL
mean_weather<-mean_weather[c(1,115:118)]
data_selag<-merge(data_selag,mean_weather,by="year")%>%
  arrange(id)%>%
  anti_join(subset(data_selag,is.na(FFD)&is.na(grazing)&
    is.na(shoot_vol)&is.na(n_fr)&is.na(n_ovules)&
    is.na(n_seeds)&is.na(n_intact_seeds)&
    is.na(n_fl)))%>% # Remove rows with all these NAs
  filter(year!=1995) # Remove data from 1995 because of problems with predation
names(data_selag)
```

```
## [1] "year"          "FFD"           "id"            "ruta"
## [5] "genet"         "data"          "vernal"        "grazing"
## [9] "shoot_vol"     "n_fr"          "n_ovules"      "FFD_corr"
## [13] "period"        "n_seeds"       "n_intact_seeds" "n_fl"
## [17] "mean_3"        "mean_4"        "mean_5"        "mean_6"
```

```
head(data_selag)
```

```
##   year      FFD      id ruta genet data      vernal      grazing shoot_vol
## 1 2006 60.00286 new_1 <NA>   NA    1 2006-03-20 18:25:00 1.00000000 1830.44
## 2 2006 58.27431 new_10 <NA>  NA    1 2006-03-20 18:25:00 0.37500000 21975.75
## 3 2007 43.03194 new_10 <NA>  NA    1 2007-03-21 00:14:00 0.00000000 19662.95
## 4 2008 44.78889 new_10 <NA>  NA    1 2008-03-20 06:04:00 0.07142857 28529.38
## 5 2009 49.54653 new_10 <NA>  NA    1 2009-03-20 11:53:00 0.92857143 1000.85
## 6 2010 57.30417 new_10 <NA>  NA    1 2010-03-20 17:42:00 0.00000000 4885.60
```

```
##   n_fr n_ovules   FFD_corr period   n_seeds n_intact_seeds n_fl   mean_3
## 1    0   0.0000      <NA>   new    0.00000    0.00000000    NA  -3.6596774
## 2   25 324.0000 2006-05-18   new  111.00000   43.48453608   180  -3.6596774
## 3    5  62.0000 2007-05-03   new   22.00000    7.00000000   290   4.1000000
## 4   18 234.5143 2008-05-04   new   89.48571   89.48571429   156   1.5870968
## 5    0   0.0000 2009-05-09   new    0.00000    0.00000000   180   0.8661290
## 6    3  32.0000 2010-05-17   new    8.00000    0.04532821    28  -0.4612903
##   mean_4 mean_5 mean_6
## 1 4.611667 10.46613 15.96333
## 2 4.611667 10.46613 15.96333
## 3 7.203333 10.94677 15.94333
## 4 6.656667 11.46935 15.54500
## 5 7.186667 11.08387 13.59667
## 6 5.285000 10.70000 15.08667
```

List of variables in data set:

- year
- FFD: first flowering date (as number of days from vernal equinox)
- id: individual identifier (including “old” for individuals in period 1987-1996 and “new” for individuals in period 2006-2017)
- ruta, genet: identifiers for plots and ids in old data
- data: 1 if data available, 0 if not
- vernal: date of vernal equinox in each year
- grazing: proportion of grazing by deer
- shoot_vol: shoot volume
- n_fr: number of fruits
- n_ovules: number of ovules
- FFD_corr: first flowering date (as a date)
- period: “old” for 1987-1996 and “new” for 2006-2017
- n_seeds: number of seeds
- n_intact_seeds: number of intact (non-predated) seeds
- n_fl: number of flowers
- mean_3/4/5/6: average of daily mean temperatures for March/April/May/June

Interactions that we will focus on:

- Seed predation: proportion of seeds escaping predation
- Grazing (by deer) before flowering: proportion of grazing

Calculate proportion of predated seeds

```
data_selag<-data_selag%>%
  mutate(prop_pred_seeds=ifelse(n_seeds==0,NA,(n_seeds-n_intact_seeds)/n_seeds),
         n_pred_seeds=n_seeds-n_intact_seeds)
```

Using only mean temperatures. Using grazing as a proportion, and for 2008-2015 use values of proportion of aboveground volume. - 1987-1996: grazing = proportion of flowers removed - 2006: grazing = proportion of grazed shoots - 2007-2015: grazing = proportion of aboveground volume removed - 2016-2017: grazing = proportion of flowers removed

Calculate successes/failures for grazing (and weights)

```

data_selag$grazing_success<-round(with(data_selag,
                                     ifelse(is.na(grazing_corr),NA,
                                             ifelse(year<1997|year>2015,
                                                    grazing_corr*n_fl,
                                                    ifelse(year>2006&year<2016,
                                                           grazing_corr*shoot_vol,
                                                           999))))))

data_selag$grazing_failure<-round(with(data_selag,
                                     ifelse(is.na(grazing_corr),NA,
                                             ifelse(year<1997|year>2015,
                                                    n_fl-grazing_success,
                                                    ifelse(year>2006&year<2016,
                                                           shoot_vol-grazing_success,
                                                           999))))))

data_selag$grazing_weights<-round(with(data_selag,
                                     ifelse(is.na(grazing_corr),NA,
                                             ifelse(year<1997|year>2015,
                                                    n_fl,
                                                    ifelse(year>2006&year<2016,
                                                           shoot_vol,
                                                           999))))))

grazing_success_2006<-read.table("data/grazing_success_2006.csv",
                                header=T,sep="," ,dec=".")
grazing_success_2006<-grazing_success_2006%>%
  mutate(weights=gr_success+gr_failure)
data_selag<-data_selag%>%
  left_join(grazing_success_2006)
data_selag$grazing_success<-with(data_selag,
                                ifelse(year==2006,gr_success,grazing_success))
data_selag$grazing_failure<-with(data_selag,
                                ifelse(year==2006,gr_failure,grazing_failure))
data_selag$grazing_weights<-with(data_selag,
                                ifelse(year==2006,weights,grazing_weights))

data_selag$gr_success<-NULL
data_selag$gr_failure<-NULL
data_selag$weights<-NULL
head(data_selag)

```

```

##   year      FFD    id ruta genet data      vernal    grazing shoot_vol
## 1 2006 60.00286 new_1 <NA>    NA      1 2006-03-20 18:25:00 1.00000000 1830.44
## 2 2006 58.27431 new_10 <NA>   NA      1 2006-03-20 18:25:00 0.37500000 21975.75
## 3 2007 43.03194 new_10 <NA>   NA      1 2007-03-21 00:14:00 0.00000000 19662.95
## 4 2008 44.78889 new_10 <NA>   NA      1 2008-03-20 06:04:00 0.07142857 28529.38
## 5 2009 49.54653 new_10 <NA>   NA      1 2009-03-20 11:53:00 0.92857143 1000.85
## 6 2010 57.30417 new_10 <NA>   NA      1 2010-03-20 17:42:00 0.00000000 4885.60
##   n_fr n_ovules  FFD_corr period  n_seeds n_intact_seeds n_fl    mean_3
## 1    0    0.0000    <NA>    new  0.00000    0.00000000    NA -3.6596774
## 2   25 324.0000 2006-05-18    new 111.00000    43.48453608  180 -3.6596774
## 3    5  62.0000 2007-05-03    new  22.00000     7.00000000  290  4.1000000
## 4   18 234.5143 2008-05-04    new  89.48571    89.48571429  156  1.5870968
## 5    0    0.0000 2009-05-09    new   0.00000    0.00000000  180  0.8661290
## 6    3  32.0000 2010-05-17    new   8.00000     0.04532821   28 -0.4612903

```

	mean_4	mean_5	mean_6	prop_pred_seeds	n_pred_seeds	grazing_new
## 1	4.611667	10.46613	15.96333	NA	0.000000	NA
## 2	4.611667	10.46613	15.96333	0.6082474	67.515464	NA
## 3	7.203333	10.94677	15.94333	0.6818182	15.000000	0.0
## 4	6.656667	11.46935	15.54500	0.0000000	0.000000	0.1
## 5	7.186667	11.08387	13.59667	NA	0.000000	0.9
## 6	5.285000	10.70000	15.08667	0.9943340	7.954672	0.0

	grazing_corr	grazing_success	grazing_failure	grazing_weights
## 1	1.000	1	0	1
## 2	0.375	3	5	8
## 3	0.000	0	19663	19663
## 4	0.100	2853	25676	28529
## 5	0.900	901	100	1001
## 6	0.000	0	4886	4886

H1 and H2: path model

H1: Flowering phenology of individuals influences the intensities of interactions with seed predators and grazers.

H2: These biotic interactions have important effects on fitness, and alter selection on flowering time within years.

Models include the effects of FFD and `n_fl` standardized within years (`FFD_s_y` and `n_fl_s_y`), grazing and seed predation on fitness relativized within years (`fitness_rel_y`), as well as the effects of `FFD_s_y` and `n_fl_s_y` on grazing and seed predation.

Calculate `FFD_s_y`, `n_fl_s_y` and `fitness_rel_y`:

```
data_selag<-data_selag%>%
  group_by(year) %>%
  mutate(FFD_mean=mean(FFD,na.rm=T),
         FFD_sd=sd(FFD,na.rm=T),
         FFD_s_y=(FFD-FFD_mean)/FFD_sd,
         n_fl_mean=mean(n_fl,na.rm=T),
         n_fl_sd=sd(n_fl,na.rm=T),
         n_fl_s_y=(n_fl-n_fl_mean)/n_fl_sd,
         fitness_mean=mean(n_intact_seeds,na.rm=T),
         fitness_rel_y=n_intact_seeds/fitness_mean)

data_selag$seeds_01<-with(data_selag,ifelse(is.na(n_seeds),NA,
                                           ifelse(n_seeds>0,1,0)))

path1_mod1<-glmmTMB(seeds_01~FFD_s_y+n_fl_s_y+grazing_corr+(1|id)+(1|year),
                    data=data_selag,family="binomial")
path1_mod2<-glmmTMB(fitness_rel_y~FFD_s_y+n_fl_s_y+grazing_corr+prop_pred_seeds+
                    (1|id)+(1|year),data=data_selag)
path1_mod3<-glmmTMB(grazing_corr~FFD_s_y+n_fl_s_y+(1|id)+(1|year),
                    data=data_selag,family="binomial",weights=grazing_weights)
path1_mod4<-glmmTMB(prop_pred_seeds~FFD_s_y+n_fl_s_y+(1|id)+(1|year),
                    data=data_selag,family="binomial",
                    weights=round(n_seeds))
```

```
nobs(path1_mod1)
```

```
## [1] 2376
```

```
nobs(path1_mod2)
```

```
## [1] 1281
```

```
nobs(path1_mod3)
```

```
## [1] 2354
```

```
nobs(path1_mod4)
```

```
## [1] 1281
```

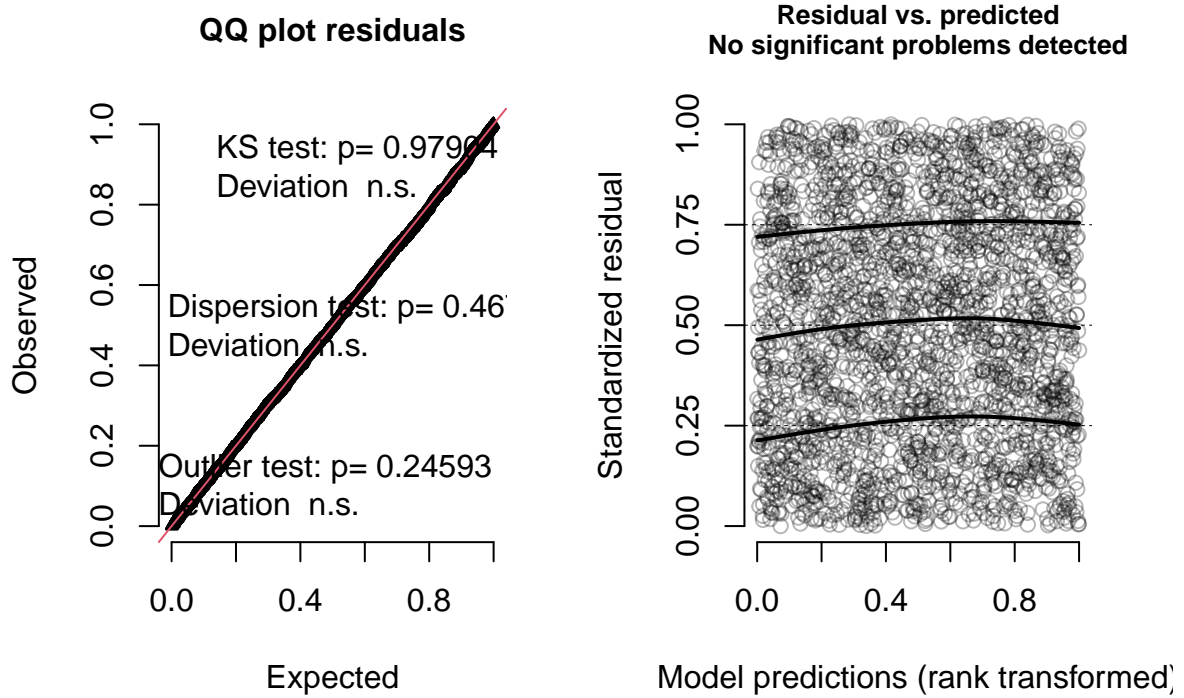
Model diagnostics

```
sim_path1_mod1 <- simulateResiduals(fittedModel = path1_mod1, n = 5000)
sim_path1_mod2 <- simulateResiduals(fittedModel = path1_mod2, n = 5000)
sim_path1_mod3 <- simulateResiduals(fittedModel = path1_mod3, n = 5000)
sim_path1_mod4 <- simulateResiduals(fittedModel = path1_mod4, n = 5000)
```

qq-plot and plot of residuals vs. predicted:

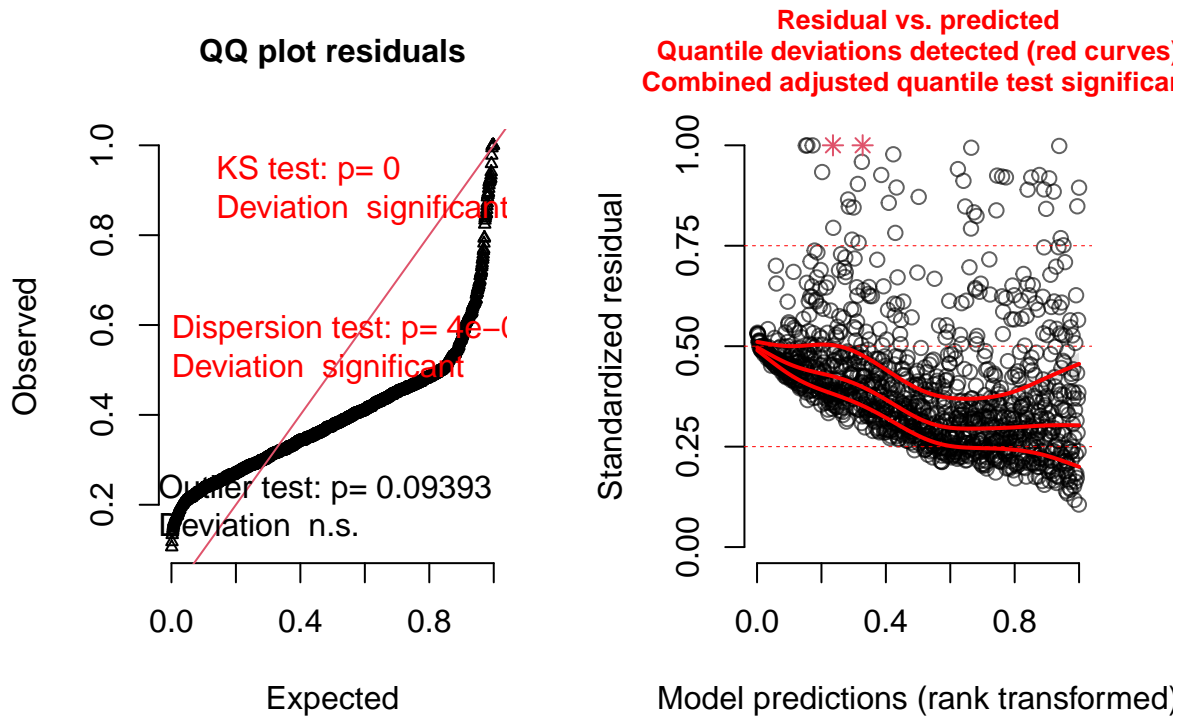
```
plot(sim_path1_mod1, quantreg=T) # model OK
```

DHARMA residual diagnostics



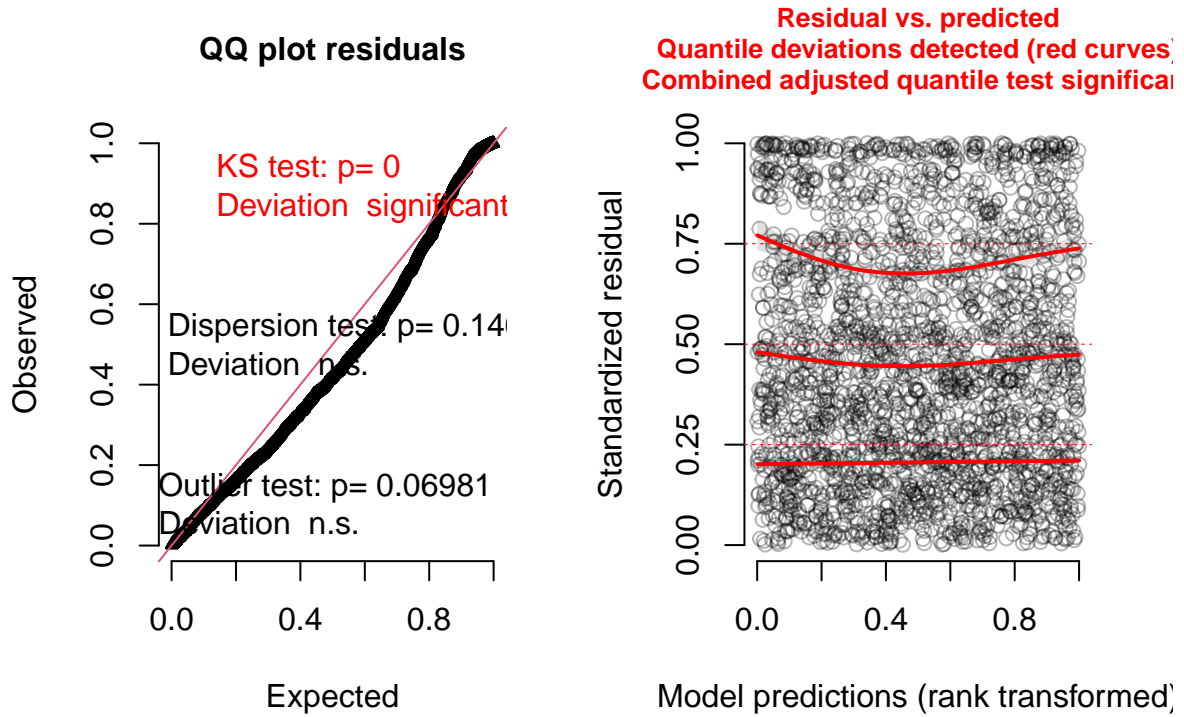
```
plot(sim_path1_mod2, quantreg=T) # not OK - calculate BCA intervals
```

DHARMA residual diagnostics



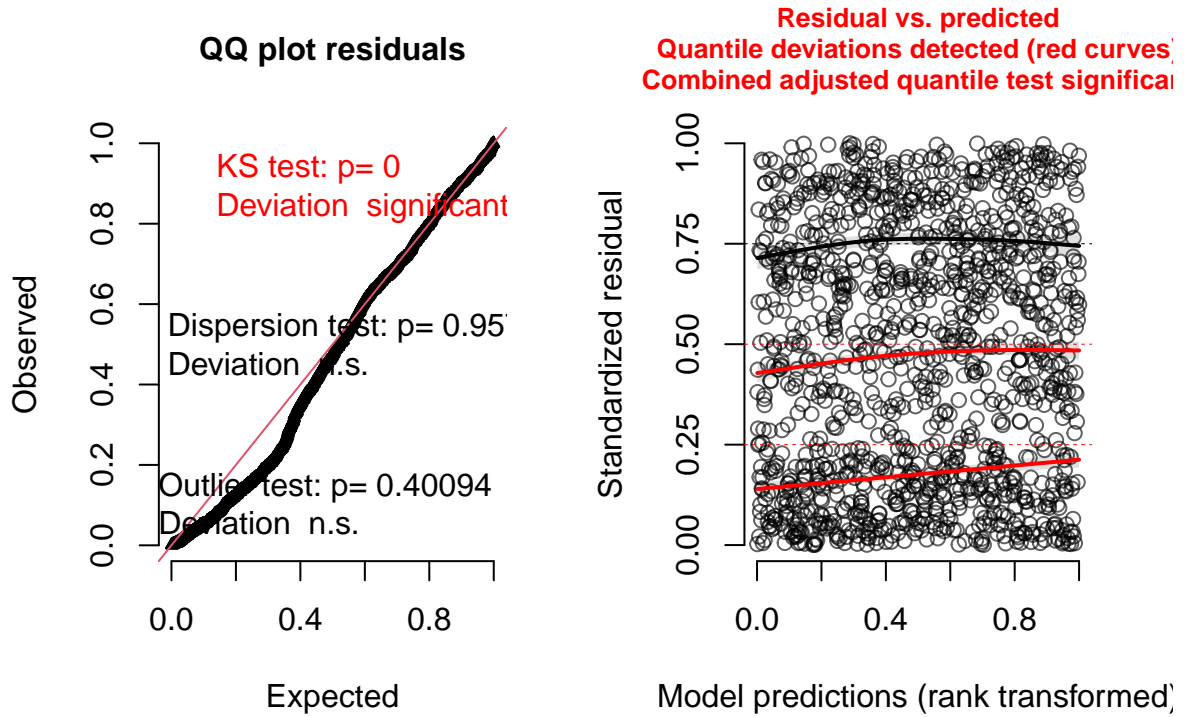
```
plot(sim_path1_mod3, quantreg=T) # not OK
```

DHARMA residual diagnostics



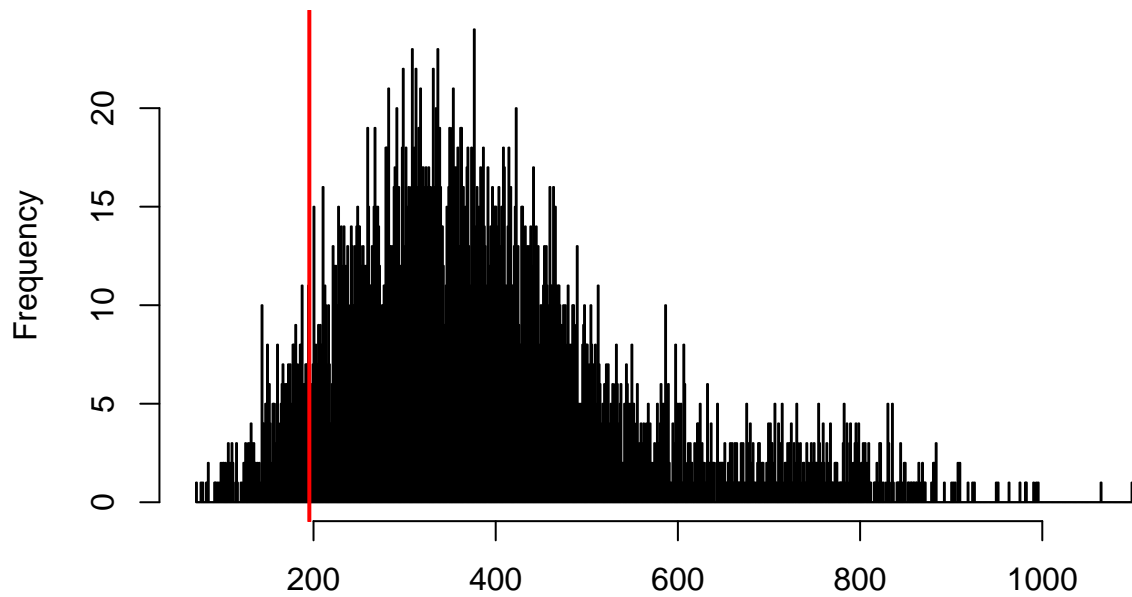
```
plot(sim_path1_mod4,quantreg=T) # not OK
```


DHARMA residual diagnostics



```
testDispersion(sim_path1_mod3) # OK
```

DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated

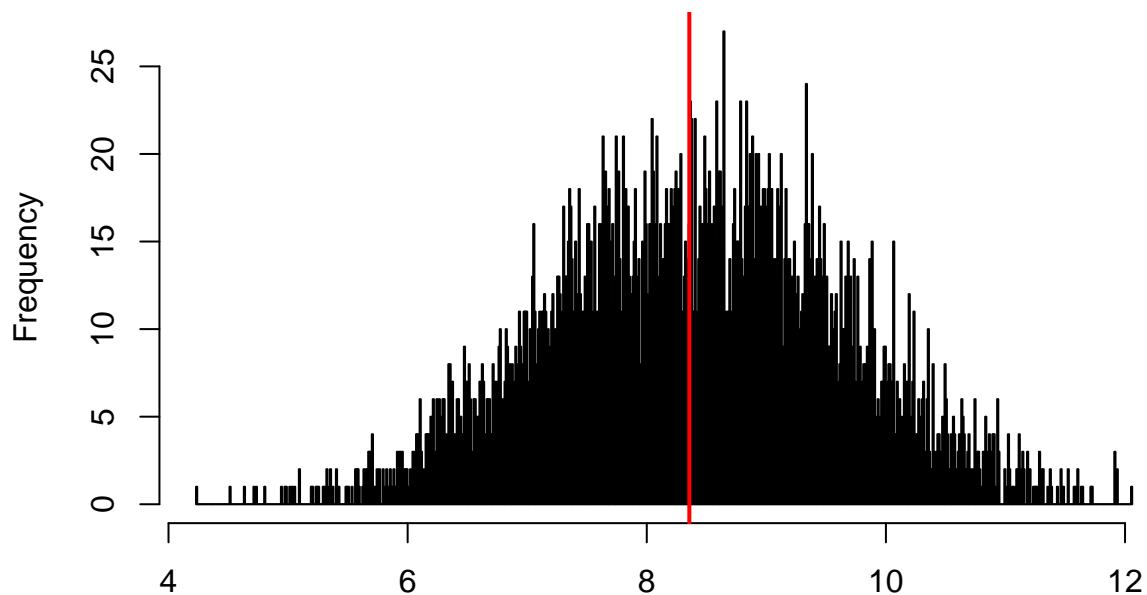


Simulated values, red line = fitted model. p-value (two.sided) = 0.1464

```
##
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.
## simulated
##
## data: simulationOutput
## ratioObsSim = 0.50412, p-value = 0.1464
## alternative hypothesis: two.sided
```

```
testDispersion(sim_path1_mod4) # OK
```

DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated

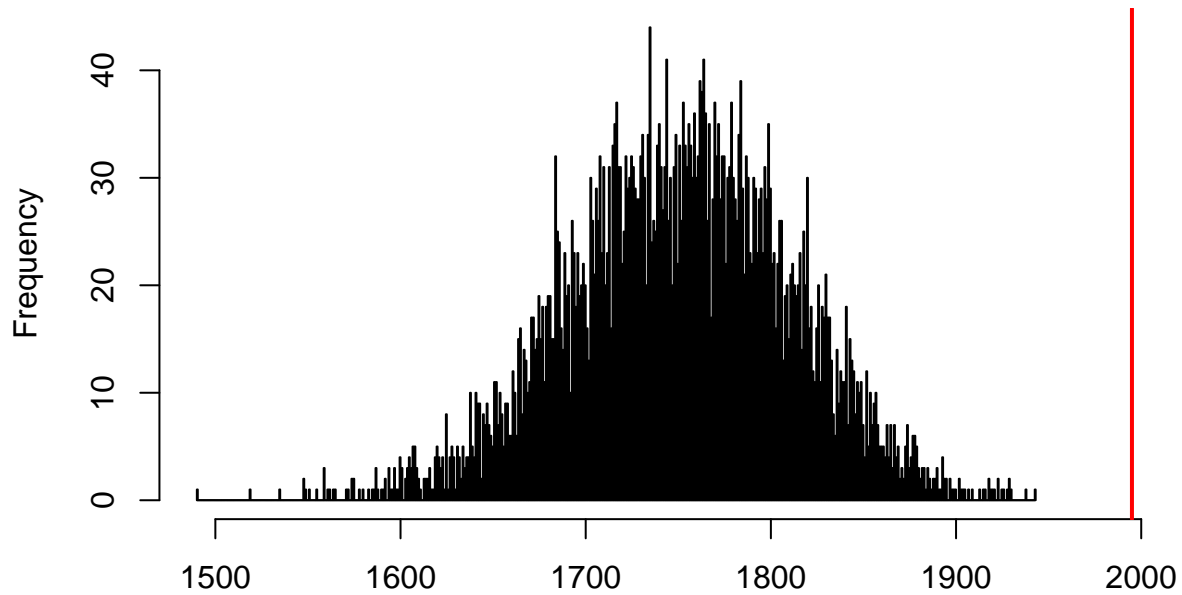


Simulated values, red line = fitted model. p-value (two.sided) = 0.9576

```
##
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.
## simulated
##
## data: simulationOutput
## ratioObsSim = 0.99474, p-value = 0.9576
## alternative hypothesis: two.sided
```

```
testZeroInflation(sim_path1_mod3) # significant
```

**DHARMA zero-inflation test via comparison to
expected zeros with simulation under H0 = fitted
model**

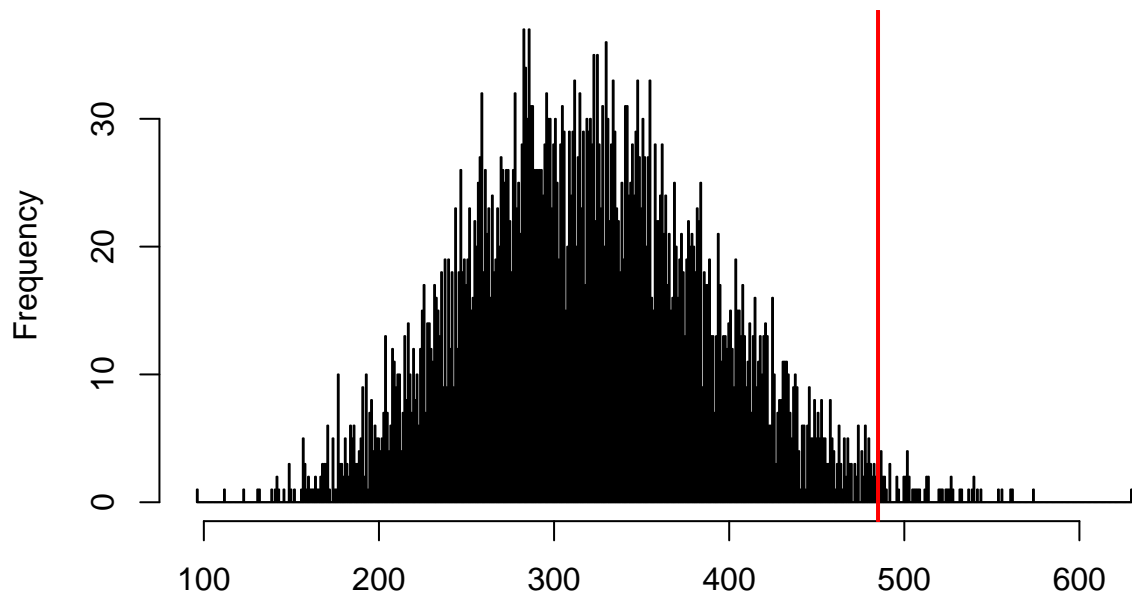


Simulated values, red line = fitted model. p-value (two.sided) = 0

```
##  
## DHARMA zero-inflation test via comparison to expected zeros with  
## simulation under H0 = fitted model  
##  
## data: simulationOutput  
## ratioObsSim = 1.1394, p-value < 2.2e-16  
## alternative hypothesis: two.sided
```

```
testZeroInflation(sim_path1_mod4) # significant
```

DHARMA zero-inflation test via comparison to expected zeros with simulation under H0 = fitted model



Simulated values, red line = fitted model. p-value (two.sided) = 0.0256

```
##
## DHARMA zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.5119, p-value = 0.0256
## alternative hypothesis: two.sided
```

Refit models 3 and 4 with betabinomial distribution.

```
path1_mod3_bb<-glmmTMB(grazing_corr~FFD_s_y+n_fl_s_y+(1|id)+(1|year),
                      data=data_selag,family="betabinomial",
                      weights=grazing_weights)
path1_mod4_bb<-glmmTMB(prop_pred_seeds~FFD_s_y+n_fl_s_y+(1|id)+(1|year),
                      data=data_selag,family="betabinomial",
                      weights=round(n_seeds))
```

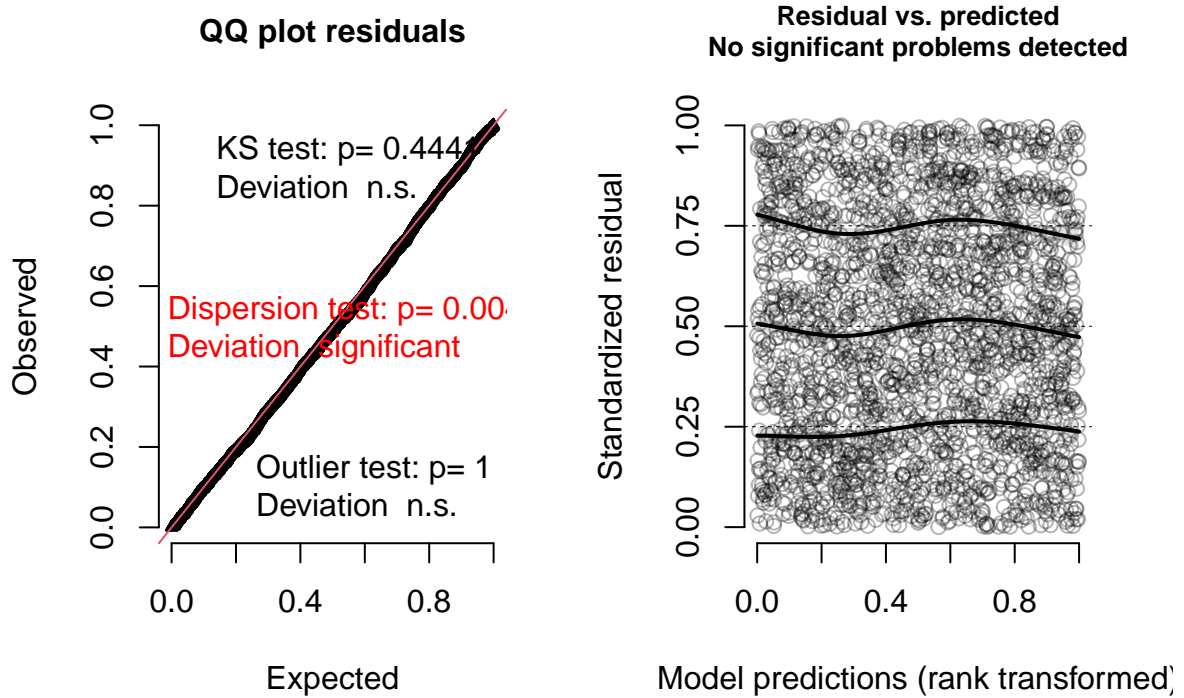
Model diagnostics

```
sim_path1_mod3_bb <- simulateResiduals(fittedModel = path1_mod3_bb, n = 5000)
sim_path1_mod4_bb <- simulateResiduals(fittedModel = path1_mod4_bb, n = 5000)
```

qq-plot and plot of residuals vs. predicted:

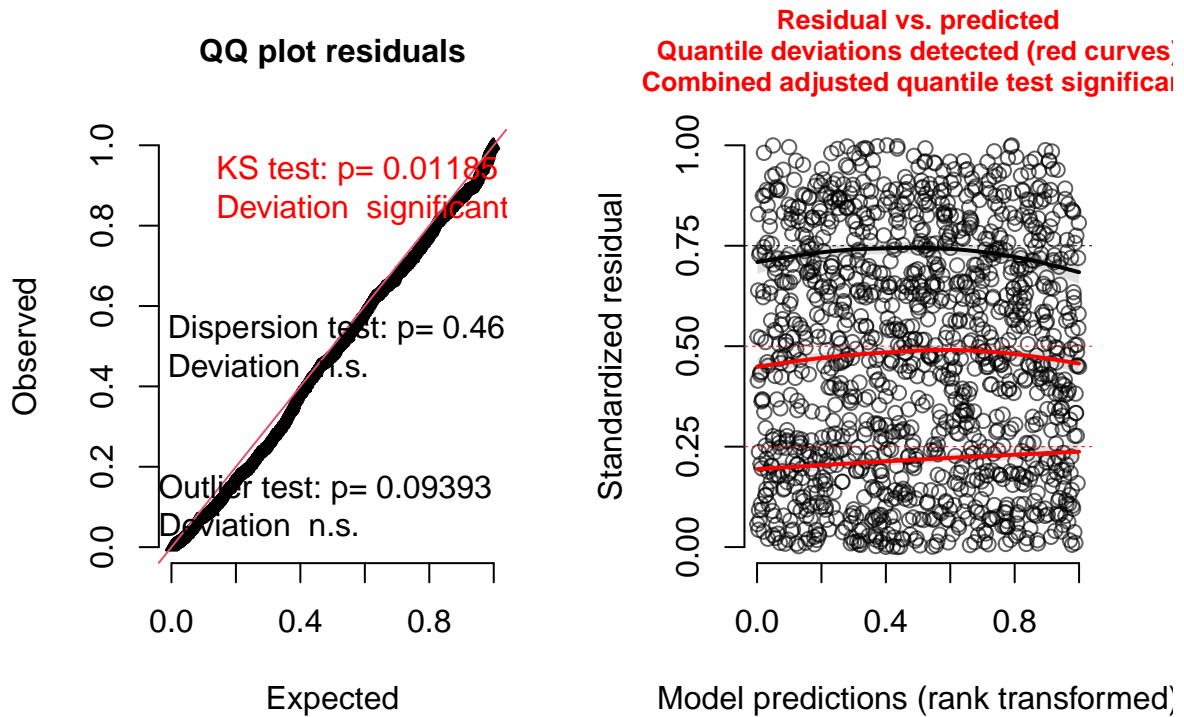
```
plot(sim_path1_mod3_bb,quantreg=T) # not OK
```

DHARMA residual diagnostics



```
plot(sim_path1_mod4_bb,quantreg=T) # not OK
```

DHARMA residual diagnostics



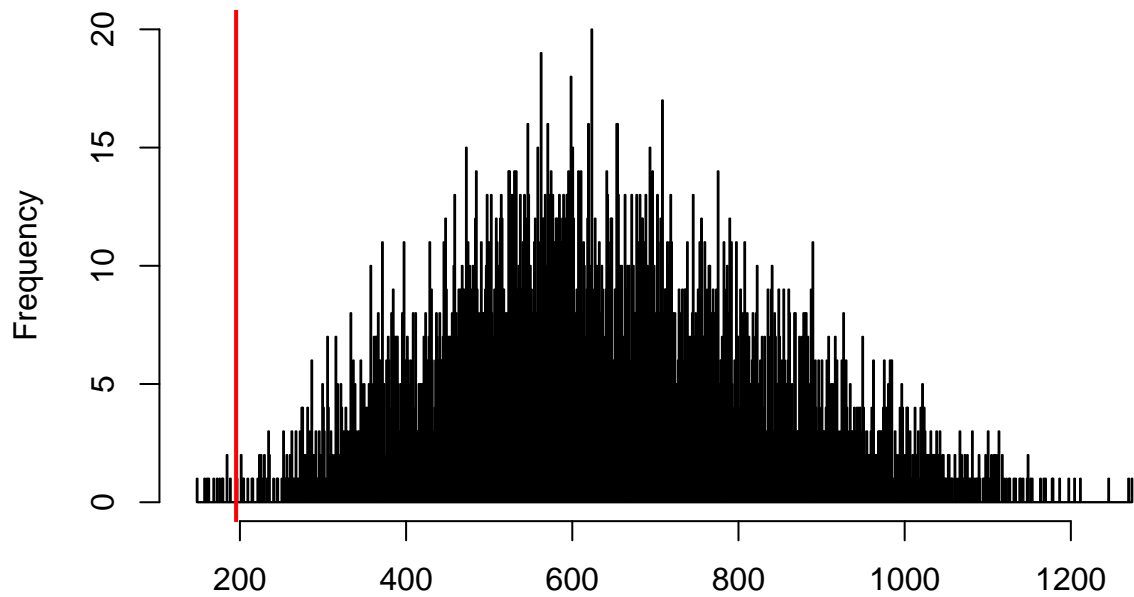
KS test being significant is probably not a problem.

From <https://github.com/florianhartig/DHARMA/issues/181>

"the p-value shows you that there is a significant deviation from the assumed distribution, but significance \neq effect size. In other words, if you have a large number of data points (as you have here), even the slightest deviation will become significant. [...] the qq-plot is nearly linear, suggesting that the overall distribution is roughly OK.

```
testDispersion(sim_path1_mod3_bb) # a bit of underdispersion, probably OK
```

**DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated**

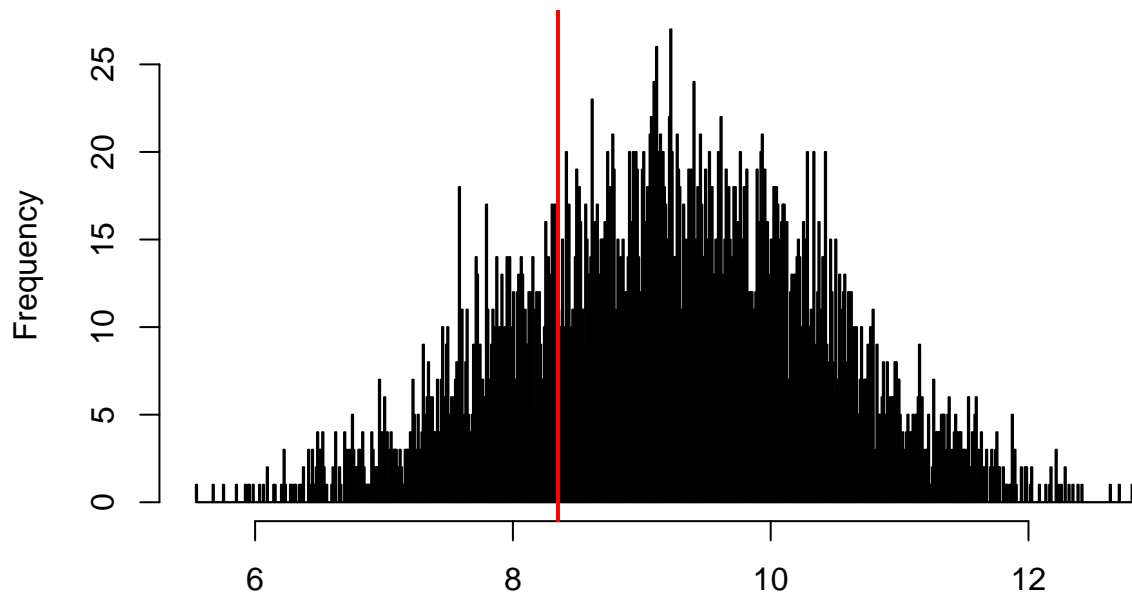


Simulated values, red line = fitted model. p-value (two.sided) = 0.0048

```
##
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.
## simulated
##
## data: simulationOutput
## ratioObsSim = 0.30572, p-value = 0.0048
## alternative hypothesis: two.sided
```

```
testDispersion(sim_path1_mod4_bb) # OK
```


DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated

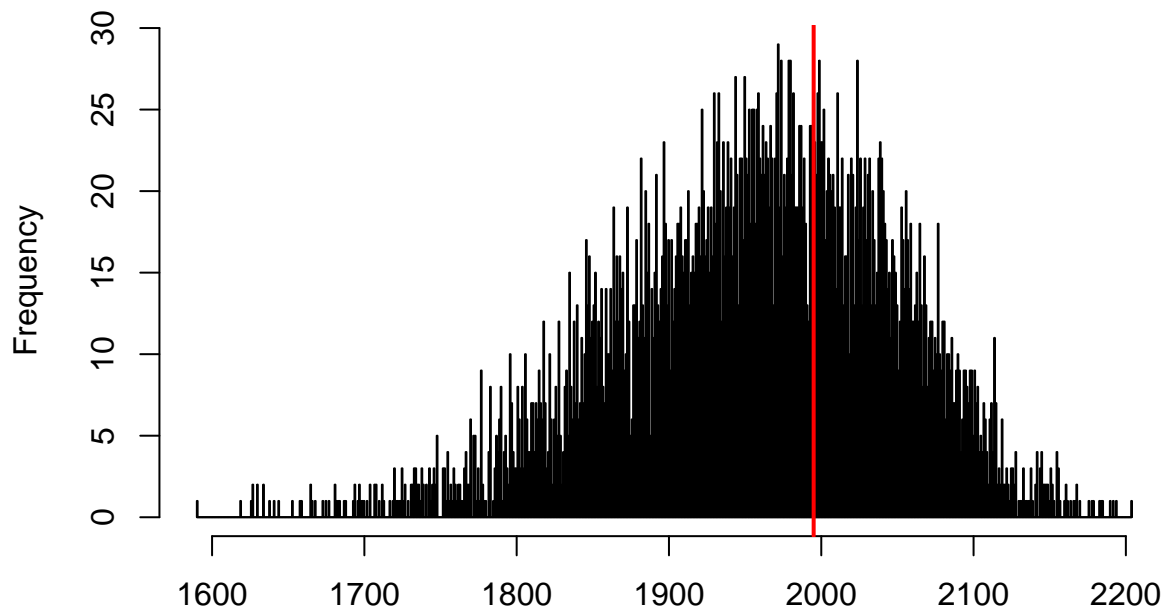


Simulated values, red line = fitted model. p-value (two.sided) = 0.4612

```
##  
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.  
## simulated  
##  
## data: simulationOutput  
## ratioObsSim = 0.90432, p-value = 0.4612  
## alternative hypothesis: two.sided
```

```
testZeroInflation(sim_path1_mod3_bb) # OK
```

**DHARMa zero-inflation test via comparison to
expected zeros with simulation under H0 = fitted
model**

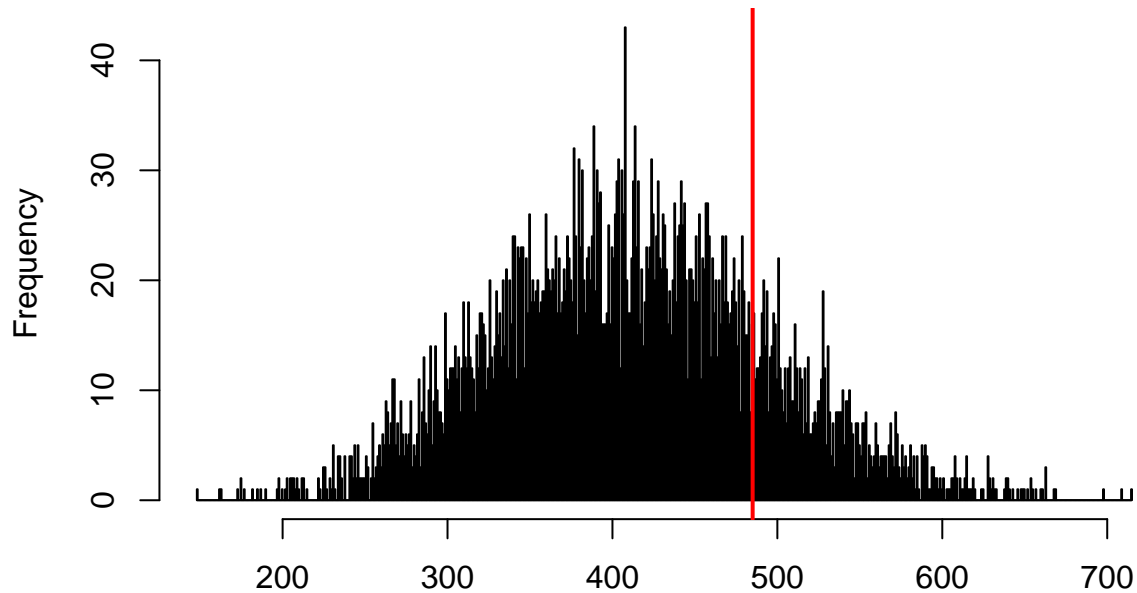


Simulated values, red line = fitted model. p-value (two.sided) = 0.7276

```
##
## DHARMa zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.0197, p-value = 0.7276
## alternative hypothesis: two.sided
```

```
testZeroInflation(sim_path1_mod4_bb) # OK
```

**DHARMa zero-inflation test via comparison to
expected zeros with simulation under H0 = fitted
model**



Simulated values, red line = fitted model. p-value (two.sided) = 0.3752

```
##
## DHARMa zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.1793, p-value = 0.3752
## alternative hypothesis: two.sided
```

```
anova(path1_mod3,path1_mod3_bb)
```

```
## Data: data_selag
## Models:
## path1_mod3: grazing_corr ~ FFD_s_y + n_fl_s_y + (1 | id) + (1 | year), zi=~0, disp=~1
## path1_mod3_bb: grazing_corr ~ FFD_s_y + n_fl_s_y + (1 | id) + (1 | year), zi=~0, disp=~1
##           Df    AIC    BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## path1_mod3    5 155103 155132 -77547   155093
## path1_mod3_bb  6   3601   3636  -1795    3589 151504      1 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
anova(path1_mod4,path1_mod4_bb)
```

```
## Data: data_selag
## Models:
```

```
## path1_mod4: prop_pred_seeds ~ FFD_s_y + n_fl_s_y + (1 | id) + (1 | year), zi=~0, disp=~1
## path1_mod4_bb: prop_pred_seeds ~ FFD_s_y + n_fl_s_y + (1 | id) + (1 | year), zi=~0, disp=~1
##           Df      AIC      BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## path1_mod4      5 6696.0 6721.8 -3343.0 6686.0
## path1_mod4_bb  6 4953.5 4984.4 -2470.8 4941.5 1744.5      1 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
AIC(path1_mod3,path1_mod3_bb)
```

```
##           df      AIC
## path1_mod3      5 155103.361
## path1_mod3_bb  6  3601.166
```

```
AIC(path1_mod4,path1_mod4_bb)
```

```
##           df      AIC
## path1_mod4      5 6695.992
## path1_mod4_bb  6 4953.500
```

Use betabinomial models.

Tested quadratic effects of FFD on grazing and seed predation, and they were not significant in betabinomial models.

Boostrapped confidence intervals for model 2:

Mixed model

```
path1_mod2_glmmer<-glmer(fitness_rel_y~FFD_s_y+n_fl_s_y+grazing_corr+
                        prop_pred_seeds+(1|id)+(1|year),data=data_selag)
# We need to use glmer for this
```

```
confint(b_par_1,level=0.95, method="boot") # Percentile method
```

```
##           2.5 %      97.5 %
## (Intercept)  2.3664280  5.93437756
## FFD_s_y      -0.3156583 -0.04331491
## n_fl_s_y      0.4743067  0.69936623
## grazing_corr -2.1922090 -0.53065021
## prop_pred_seeds -4.0396053 -3.24794402
```

Similar to significances in the lmer model.

LM (Elsa's code) (not used)

Similar to significances in the lmer model except for grazing, where the CIs overlap zero here. Use only percentile method?

New path model

```
summary(path1_mod1)$coefficients
```

```
## $cond
##           Estimate Std. Error    z value    Pr(>|z|)
## (Intercept)  0.5448470 0.21257583   2.563071 1.037508e-02
## FFD_s_y      -0.6968366 0.06747741 -10.326961 5.321988e-25
## n_fl_s_y      0.6111297 0.07683091   7.954216 1.802689e-15
## grazing_corr -3.8250266 0.32225988 -11.869385 1.707182e-32
##
## $zi
## NULL
##
## $disp
## NULL
```

```
# std coefs if needed from path1 without random effects
```

```
summary(path1_mod2)$coefficients
```

```
## $cond
##           Estimate Std. Error    z value    Pr(>|z|)
## (Intercept)  4.1866333 0.88694757   4.720271 2.355301e-06
## FFD_s_y      -0.1790698 0.06873317  -2.605290 9.179656e-03
## n_fl_s_y      0.5868972 0.05766612  10.177505 2.498870e-24
## grazing_corr  -1.3597652 0.42561090  -3.194855 1.399010e-03
## prop_pred_seeds -3.6442115 0.20386754 -17.875388 1.833937e-71
##
## $zi
## NULL
##
## $disp
## NULL
```

```
# get significances from bootstrapped CIs, std coefs from path1 without random effects
```

```
summary(path1_mod3_bb)$coefficients
```

```
## $cond
##           Estimate Std. Error    z value    Pr(>|z|)
## (Intercept) -2.9368887 0.32909846  -8.924043 4.495707e-19
## FFD_s_y      -0.3479031 0.08335881  -4.173561 2.998753e-05
## n_fl_s_y      0.1875620 0.06457848   2.904404 3.679536e-03
##
## $zi
## NULL
##
## $disp
## NULL
```

```
# significances and ustd coefs from here, std if needed from path1 without random effects
summary(path1_mod4_bb)$coefficients
```

```
## $cond
##           Estimate Std. Error   z value    Pr(>|z|)
## (Intercept) -0.7491371 0.31175650 -2.402956 1.626315e-02
## FFD_s_y      0.1007740 0.05463502  1.844495 6.511103e-02
## n_fl_s_y     0.2060346 0.04261941  4.834291 1.336212e-06
##
## $zi
## NULL
##
## $disp
## NULL
```

```
# significances and ustd coefs from here, std if needed from path1 without random effects
```

piecewiseSEM does not work with glmmTMB - and that is the only package I found that fits betabinomial mixed models.

```
path1_norandom<-psem(
  glm(seeds_01~FFD_s_y+n_fl_s_y+grazing_corr,
      data=data_selag,family="binomial"),
  lm(fitness_rel_y~FFD_s_y+n_fl_s_y+grazing_corr+prop_pred_seeds,
     data=data_selag),
  glm(grazing_corr~FFD_s_y+n_fl_s_y,
      data=data_selag,family="binomial",weights=grazing_weights),
  glm(prop_pred_seeds~FFD_s_y+n_fl_s_y,
      data=data_selag,family="binomial",
      weights=n_seeds))
coefs(path1_norandom)
```

	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value
## 1	seeds_01	FFD_s_y	-0.6041	0.0559	2372	-10.8057	0.0000
## 2	seeds_01	n_fl_s_y	0.4999	0.0642	2372	7.7907	0.0000
## 3	seeds_01	grazing_corr	-3.2497	0.2395	2372	-13.5712	0.0000
## 4	fitness_rel_y	FFD_s_y	-0.2054	0.0881	1276	-2.3322	0.0198
## 5	fitness_rel_y	n_fl_s_y	0.4506	0.0726	1276	6.2070	0.0000
## 6	fitness_rel_y	grazing_corr	0.6428	0.5272	1276	1.2192	0.2230
## 7	fitness_rel_y	prop_pred_seeds	-1.6647	0.1931	1276	-8.6187	0.0000
## 8	grazing_corr	FFD_s_y	-0.1169	0.0054	2350	-21.5365	0.0000
## 9	grazing_corr	n_fl_s_y	-0.0692	0.0033	2350	-20.7038	0.0000
## 10	prop_pred_seeds	FFD_s_y	-0.0330	0.0208	1278	-1.5837	0.1133
## 11	prop_pred_seeds	n_fl_s_y	0.0893	0.0120	1278	7.4500	0.0000
##	Std.Estimate						
## 1	-0.2741 ***						
## 2	0.2268 ***						
## 3	-0.4572 ***						
## 4	-0.0965 *						
## 5	0.2118 ***						
## 6	0.0937						
## 7	-0.2859 ***						

```
## 8      -0.0641 ***
## 9      -0.0379 ***
## 10     -0.0181
## 11      0.0490 ***
```

```
plot(path1_norandom)
```

Figure 1: Path diagram (made in Inkscape)

% of grazed plants that produced seeds

```
nrow(subset(data_selag,grazing_corr>0&n_seeds>0))*100/
  nrow(subset(data_selag,grazing_corr>0))
```

```
## [1] 28.63341
```

% of plants with more than half of their above-ground structures removed that produced seeds

```
nrow(subset(data_selag,grazing_corr>0.5&n_seeds>0))*100/
  nrow(subset(data_selag,grazing_corr>0))
```

```
## [1] 6.290672
```

Only 29% of plants that experienced any grazing produced seeds, and 6% of plants that had more than half of their above-ground structures removed.

H3

H3: Variation in climatic conditions during spring among years causes differences in selection on flowering time, through effects mediated by the intensity of biotic interactions.

H3 - Part 1

Variation in climatic conditions during spring among years influences the intensity of biotic interactions and the covariance between interaction intensity and plant phenology.

First, models to test the effect of spring temperatures on antagonistic interactions, while accounting for FFD and number of flowers. Using FFD and number of flowers standardized within years, temperatures standardized across years. Including interactions among FFD and temperatures. NOT including a random effect of year because there is only one value of temperature for each year.

Grazing

```
mod_grazing<-glmmTMB(cbind(grazing_success,grazing_failure)~
  (scale(mean_3)+scale(mean_4)+scale(mean_5))*FFD_s_y+
  n_fl_s_y+(1|id),data = data_selag,
  family="binomial")
summary(mod_grazing)
```

```

## Family: binomial ( logit )
## Formula:
## cbind(grazing_success, grazing_failure) ~ (scale(mean_3) + scale(mean_4) +
##       scale(mean_5)) * FFD_s_y + n_fl_s_y + (1 | id)
## Data: data_selag
##
##      AIC      BIC   logLik deviance df.resid
## 174950.7 175008.3 -87465.4 174930.7      2344
##
## Random effects:
##
## Conditional model:
##   Groups Name      Variance Std.Dev.
##   id      (Intercept) 48.66    6.976
## Number of obs: 2354, groups: id, 834
##
## Conditional model:
##               Estimate Std. Error z value Pr(>|z|)
## (Intercept)      -8.990310   0.459323  -19.57 < 2e-16 ***
## scale(mean_3)       0.683845   0.007932   86.21 < 2e-16 ***
## scale(mean_4)       0.022606   0.005433    4.16 3.17e-05 ***
## scale(mean_5)      -0.066343   0.028336   -2.34 0.0192 *
## FFD_s_y            -0.942016   0.015389  -61.22 < 2e-16 ***
## n_fl_s_y           -0.182051   0.005101  -35.69 < 2e-16 ***
## scale(mean_3):FFD_s_y 0.522687   0.008510   61.42 < 2e-16 ***
## scale(mean_4):FFD_s_y 0.168588   0.005916   28.50 < 2e-16 ***
## scale(mean_5):FFD_s_y 1.788498   0.031905   56.06 < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Model diagnostics

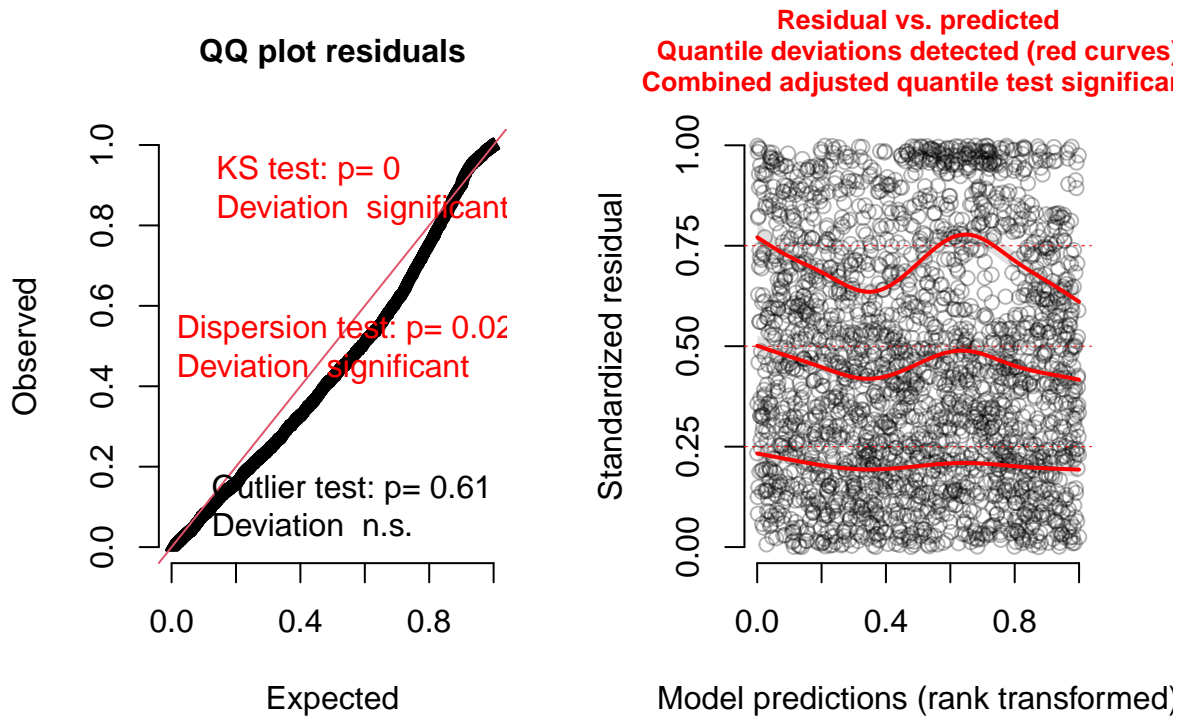
Simulate residuals of the model:

```
sim_mod_grazing <- simulateResiduals(fittedModel=mod_grazing,n=5000)
```

qq-plot and plot of residuals vs. predicted:

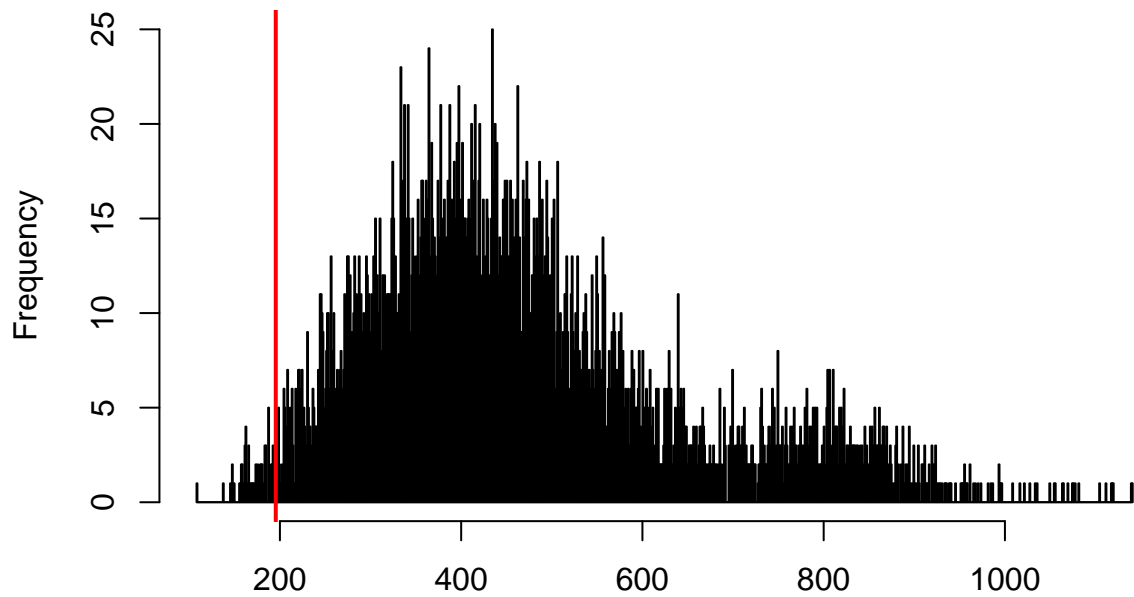
```
plot(sim_mod_grazing,quantreg=T)
```


DHARMA residual diagnostics



```
testDispersion(sim_mod_grazing)
```

**DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated**



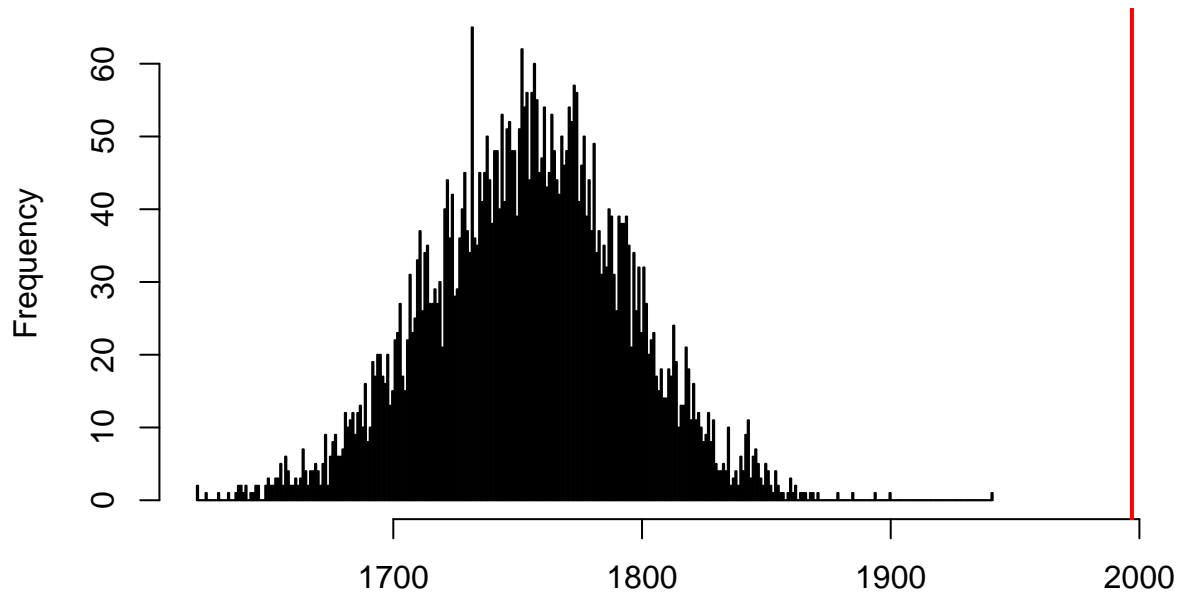
Simulated values, red line = fitted model. p-value (two.sided) = 0.026

```
##  
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.  
## simulated  
##  
## data: simulationOutput  
## ratioObsSim = 0.41949, p-value = 0.026  
## alternative hypothesis: two.sided
```

Slightly underdispersed.

```
testZeroInflation(sim_mod_grazing)
```

DHARMA zero-inflation test via comparison to expected zeros with simulation under H0 = fitted model



Simulated values, red line = fitted model. p-value (two.sided) = 0

```
##
## DHARMA zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.1381, p-value < 2.2e-16
## alternative hypothesis: two.sided
```

Test of zero inflation is significant.

Try with betabinomial

```
mod_grazing_bb<-glmmTMB(cbind(grazing_success,grazing_failure)~
  (scale(mean_3)+scale(mean_4)+scale(mean_5))*FFD_s_y+
  n_fl_s_y+(1|id),data = data_selag,
  family="betabinomial")
summary(mod_grazing_bb)

## Family: betabinomial ( logit )
## Formula:
## cbind(grazing_success, grazing_failure) ~ (scale(mean_3) + scale(mean_4) +
##       scale(mean_5)) * FFD_s_y + n_fl_s_y + (1 | id)
## Data: data_selag
```

```
##
##      AIC      BIC   logLik deviance df.resid
##  4013.7   4077.1 -1995.8   3991.7     2343
##
## Random effects:
##
## Conditional model:
##   Groups Name      Variance Std.Dev.
##   id      (Intercept) 0.2367   0.4865
## Number of obs: 2354, groups: id, 834
##
## Overdispersion parameter for betabinomial family (): 0.141
##
## Conditional model:
##               Estimate Std. Error z value Pr(>|z|)
## (Intercept)      -2.23190    0.09050 -24.663 < 2e-16 ***
## scale(mean_3)       0.50384    0.06704   7.516 5.66e-14 ***
## scale(mean_4)      -0.33282    0.06416  -5.187 2.14e-07 ***
## scale(mean_5)      -0.44010    0.08623  -5.104 3.32e-07 ***
## FFD_s_y            -0.25577    0.07307  -3.500 0.000464 ***
## n_fl_s_y           0.15921    0.05901   2.698 0.006976 **
## scale(mean_3):FFD_s_y 0.10707    0.07179   1.491 0.135832
## scale(mean_4):FFD_s_y -0.12757    0.06553  -1.947 0.051571 .
## scale(mean_5):FFD_s_y 0.02182    0.08916   0.245 0.806639
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Model diagnostics

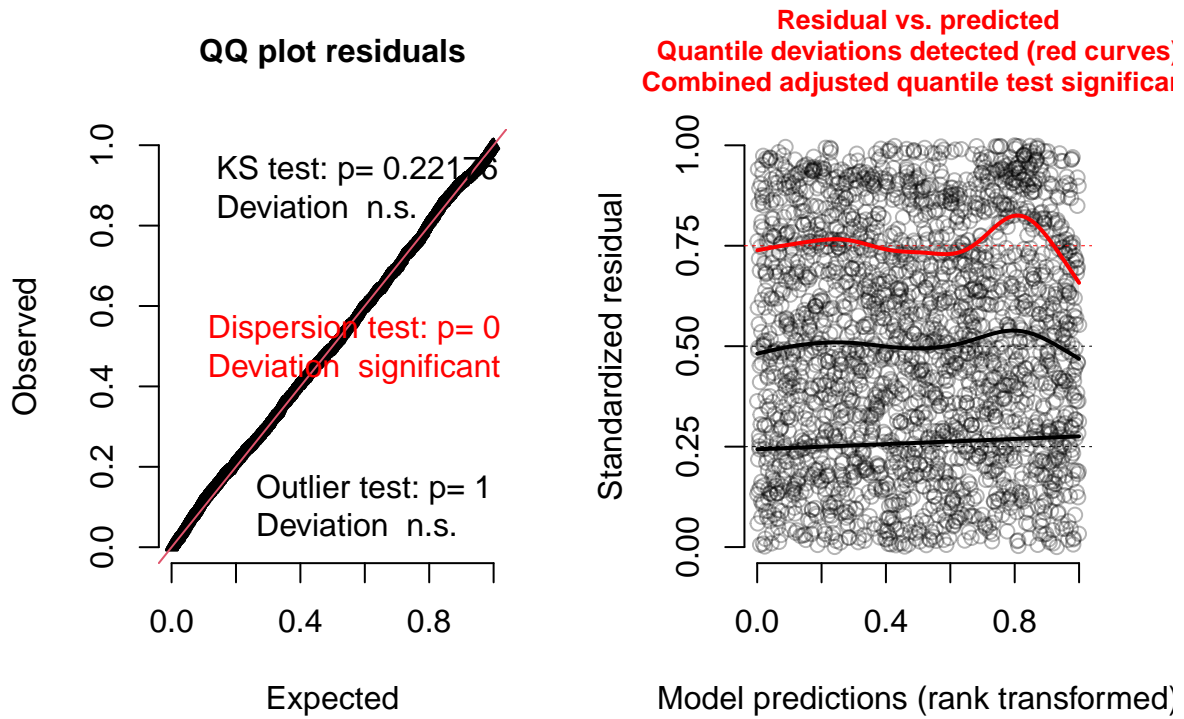
Simulate residuals of the model:

```
sim_mod_grazing_bb <- simulateResiduals(fittedModel=mod_grazing_bb,n=5000)
```

qq-plot and plot of residuals vs. predicted:

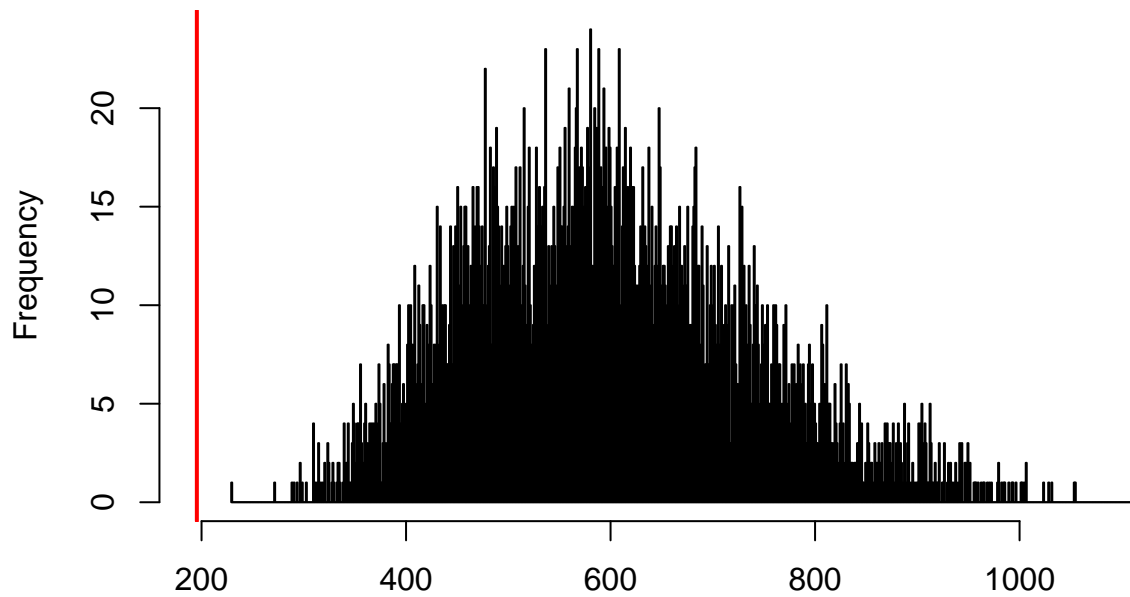
```
plot(sim_mod_grazing_bb,quantreg=T)
```

DHARMA residual diagnostics



```
testDispersion(sim_mod_grazing_bb)
```

**DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated**



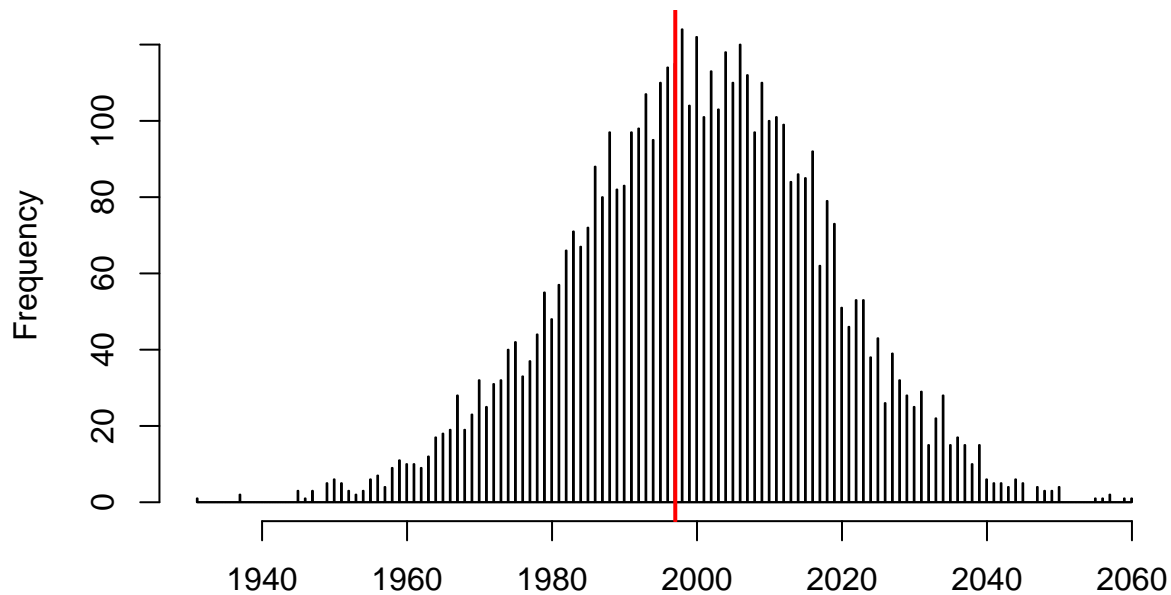
Simulated values, red line = fitted model. p-value (two.sided) = 0

```
##
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.
## simulated
##
## data: simulationOutput
## ratioObsSim = 0.32727, p-value < 2.2e-16
## alternative hypothesis: two.sided
```

Still underdispersion.

```
testZeroInflation(sim_mod_grazing_bb)
```

DHARMA zero-inflation test via comparison to expected zeros with simulation under H0 = fitted model



Simulated values, red line = fitted model. p-value (two.sided) = 0.8616

```
##
## DHARMA zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 0.9984, p-value = 0.8616
## alternative hypothesis: two.sided
```

But zero inflation is fixed

```
anova(mod_grazing,mod_grazing_bb)
```

```
## Data: data_selag
## Models:
## mod_grazing: cbind(grazing_success, grazing_failure) ~ (scale(mean_3) + scale(mean_4) + , zi=~0, disp
## mod_grazing:      scale(mean_5)) * FFD_s_y + n_fl_s_y + (1 | id), zi=~0, disp=~1
## mod_grazing_bb: cbind(grazing_success, grazing_failure) ~ (scale(mean_3) + scale(mean_4) + , zi=~0, c
## mod_grazing_bb:      scale(mean_5)) * FFD_s_y + n_fl_s_y + (1 | id), zi=~0, disp=~1
##           Df    AIC    BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
## mod_grazing   10 174951 175008 -87465   174931
## mod_grazing_bb 11   4014   4077  -1996    3992 170939      1 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
AIC(mod_grazing,mod_grazing_bb)
```

```
##           df          AIC
## mod_grazing    10 174950.700
## mod_grazing_bb 11   4013.658
```

Keep mod_grazing_bb.

Seed predation

```
mod_seedpred<-glmmTMB(cbind(round(n_pred_seeds),round(n_intact_seeds))~
                      (scale(mean_3)+scale(mean_4)+scale(mean_5)+scale(mean_6))*
                      FFD_s_y+n_fl_s_y+(1|id),data=subset(data_selag,n_seeds>0),
                      family="binomial")
summary(mod_seedpred)
```

```
## Family: binomial ( logit )
## Formula:
## cbind(round(n_pred_seeds), round(n_intact_seeds)) ~ (scale(mean_3) +
##      scale(mean_4) + scale(mean_5) + scale(mean_6)) * FFD_s_y +
##      n_fl_s_y + (1 | id)
## Data: subset(data_selag, n_seeds > 0)
##
##      AIC      BIC   logLik deviance df.resid
##  9018.9   9080.7 -4497.4   8994.9     1269
##
## Random effects:
##
## Conditional model:
##      Groups Name      Variance Std.Dev.
##      id      (Intercept) 2.281    1.51
## Number of obs: 1281, groups: id, 593
##
## Conditional model:
##
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)    -1.41142    0.07781 -18.138 < 2e-16 ***
## scale(mean_3)   -0.13644    0.03757  -3.632 0.000282 ***
## scale(mean_4)   -0.25152    0.03480  -7.228 4.90e-13 ***
## scale(mean_5)    0.21985    0.04841   4.541 5.59e-06 ***
## scale(mean_6)    0.55555    0.03961  14.026 < 2e-16 ***
## FFD_s_y         0.00579    0.03651   0.159 0.873979
## n_fl_s_y        0.07319    0.02312   3.165 0.001550 **
## scale(mean_3):FFD_s_y 0.38384    0.04201   9.136 < 2e-16 ***
## scale(mean_4):FFD_s_y -0.34184    0.03692  -9.258 < 2e-16 ***
## scale(mean_5):FFD_s_y -0.03326    0.05404  -0.615 0.538252
## scale(mean_6):FFD_s_y -0.06563    0.04443  -1.477 0.139633
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```


Model diagnostics

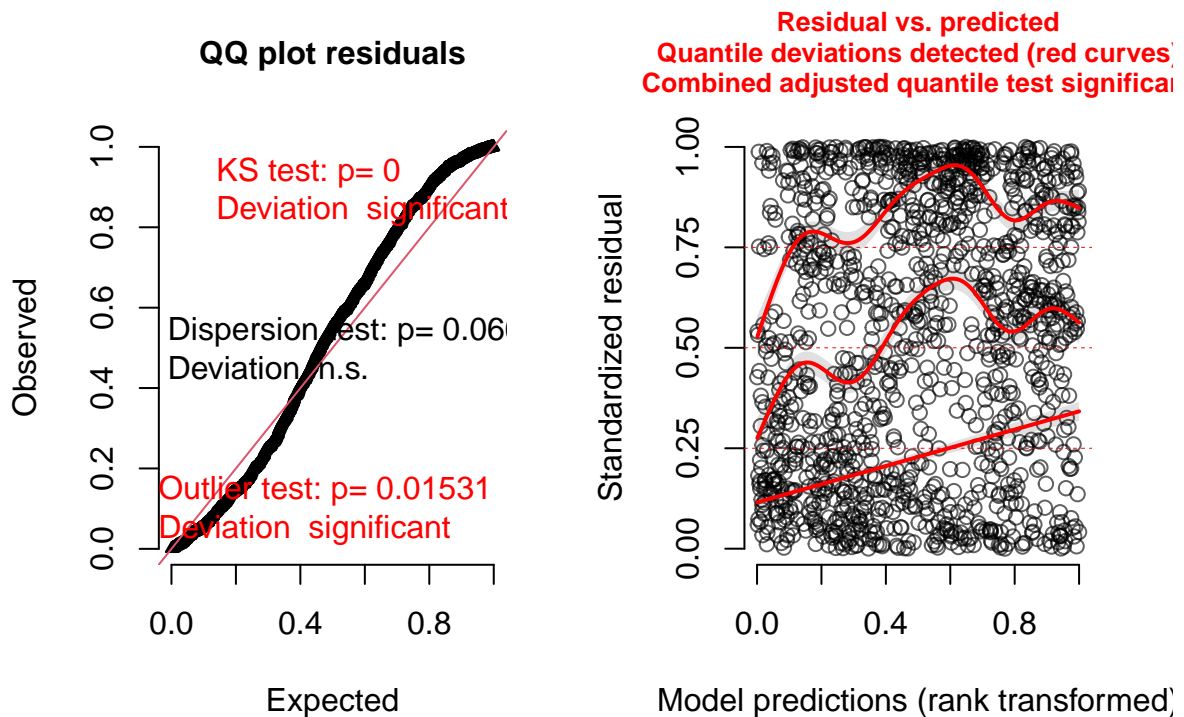
Simulate residuals of the model:

```
sim_mod_seedpred <- simulateResiduals(fittedModel=mod_seedpred,n=5000)
```

qq-plot and plot of residuals vs. predicted:

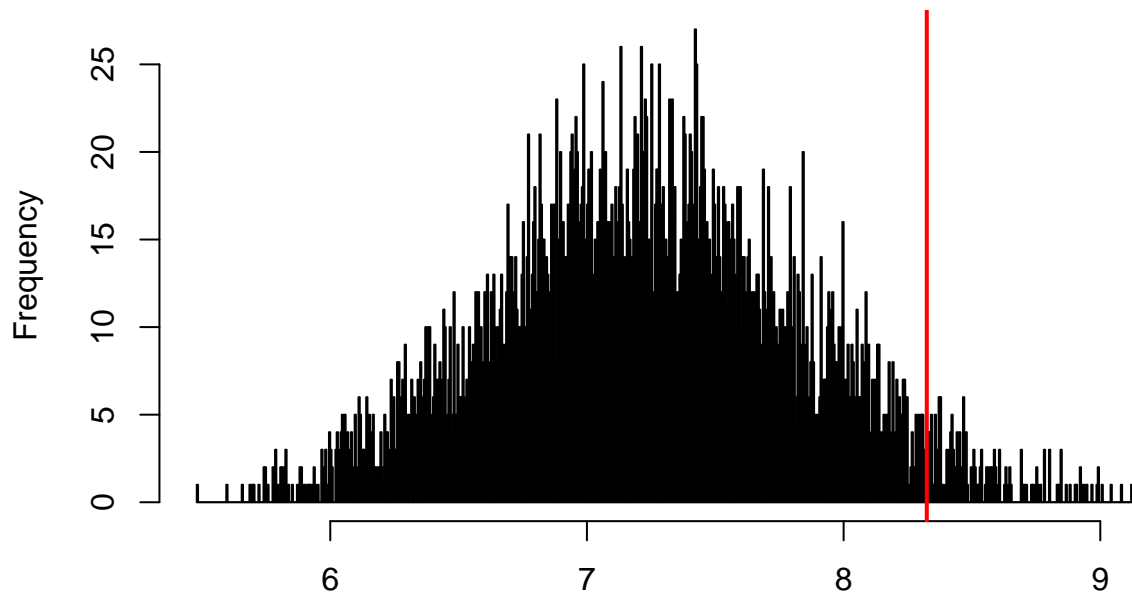
```
plot(sim_mod_seedpred,quantreg=T)
```

DHARMA residual diagnostics



```
testDispersion(sim_mod_seedpred)
```

**DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated**



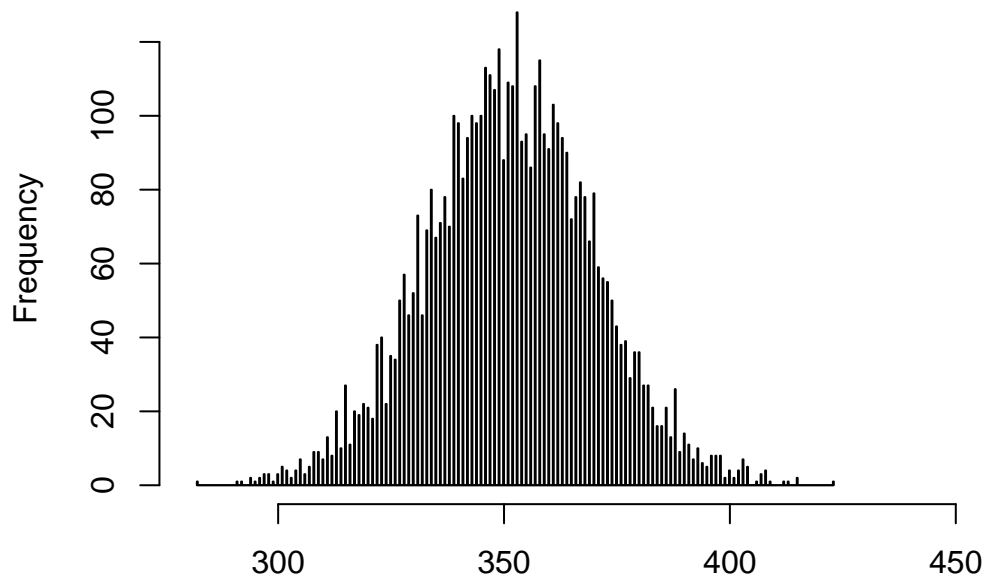
Simulated values, red line = fitted model. p-value (two.sided) = 0.0668

```
##
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.
## simulated
##
## data: simulationOutput
## ratioObsSim = 1.1495, p-value = 0.0668
## alternative hypothesis: two.sided
```

OK.

```
testZeroInflation(sim_mod_seedpred)
```

DHARMA zero-inflation test via comparison to expected zeros with simulation under H0 = fitted model



Simulated values, red line = fitted model. p-value (two.sided) = 0

```
##
## DHARMA zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.3914, p-value < 2.2e-16
## alternative hypothesis: two.sided
```

Zero inflation.

Try with betabinomial

```
mod_seedpred_bb<-glmmTMB(cbind(round(n_pred_seeds),round(n_intact_seeds))~
  (scale(mean_3)+scale(mean_4)+scale(mean_5)+scale(mean_6))*
  FFD_s_y+n_fl_s_y+(1|id),data=subset(data_selag,n_seeds>0),
  family="betabinomial")
summary(mod_seedpred_bb)
```

```
## Family: betabinomial ( logit )
## Formula:
## cbind(round(n_pred_seeds), round(n_intact_seeds)) ~ (scale(mean_3) +
##   scale(mean_4) + scale(mean_5) + scale(mean_6)) * FFD_s_y +
##   n_fl_s_y + (1 | id)
```

```
## Data: subset(data_selag, n_seeds > 0)
##
##      AIC      BIC   logLik deviance df.resid
##  5339.2   5406.3  -2656.6   5313.2     1268
##
## Random effects:
##
## Conditional model:
##   Groups Name      Variance Std.Dev.
##   id      (Intercept) 0.06597  0.2569
## Number of obs: 1281, groups: id, 593
##
## Overdispersion parameter for betabinomial family (): 1.15
##
## Conditional model:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)    -0.84346    0.05517  -15.289  < 2e-16 ***
## scale(mean_3)   -0.20163    0.07223   -2.792  0.00525 **
## scale(mean_4)    0.02973    0.06213    0.478  0.63233
## scale(mean_5)    0.46942    0.07236    6.487  8.75e-11 ***
## scale(mean_6)    0.41522    0.06211    6.685  2.31e-11 ***
## FFD_s_y         0.03140    0.05865    0.535  0.59231
## n_fl_s_y        0.17791    0.04409    4.035  5.46e-05 ***
## scale(mean_3):FFD_s_y 0.17398    0.08155    2.133  0.03289 *
## scale(mean_4):FFD_s_y -0.15858    0.06662   -2.380  0.01729 *
## scale(mean_5):FFD_s_y 0.02516    0.07756    0.324  0.74566
## scale(mean_6):FFD_s_y -0.09364    0.06820   -1.373  0.16972
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Model diagnostics

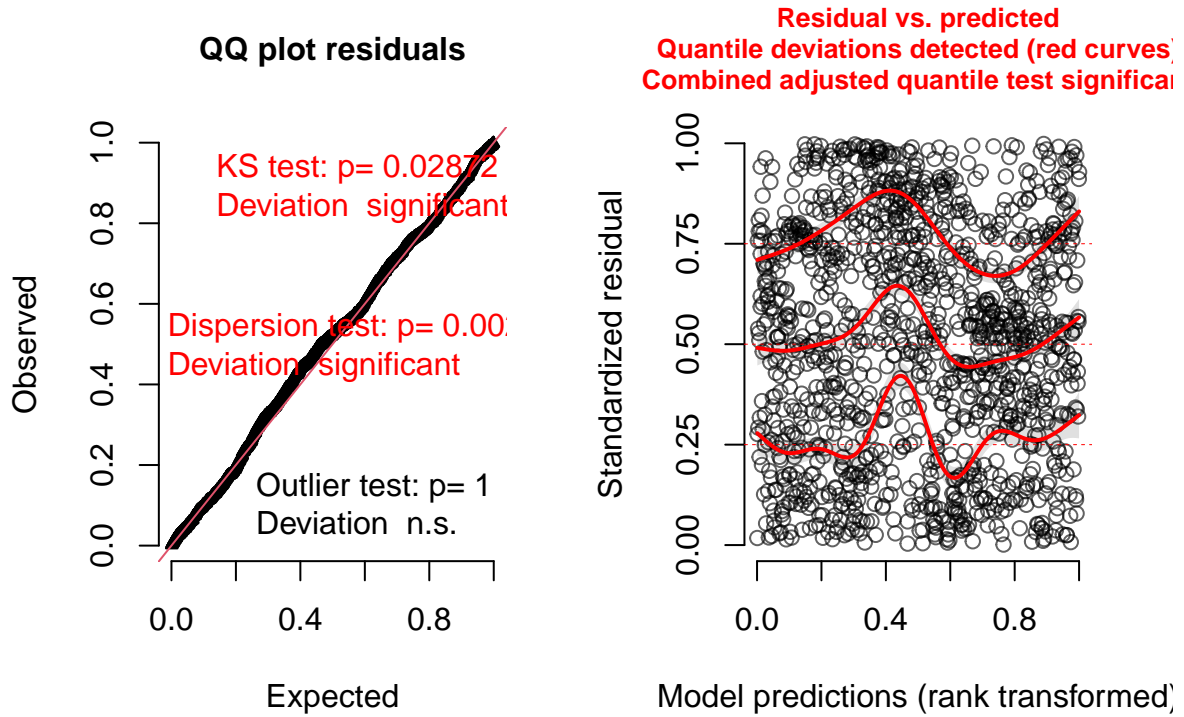
Simulate residuals of the model:

```
sim_mod_seedpred_bb <- simulateResiduals(fittedModel=mod_seedpred_bb,n=5000)
```

qq-plot and plot of residuals vs. predicted:

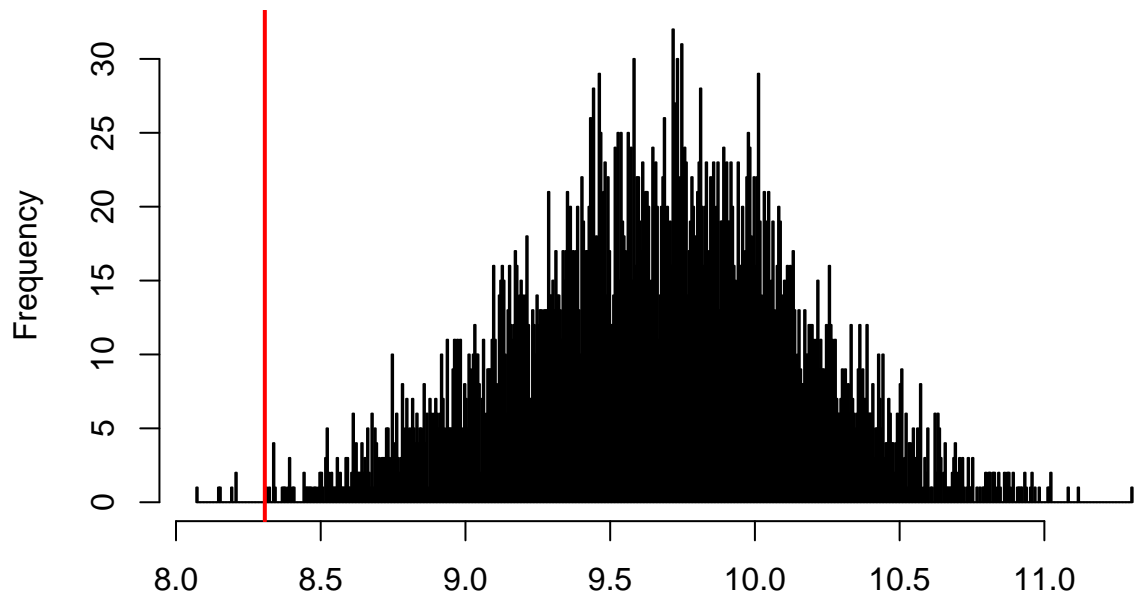
```
plot(sim_mod_seedpred_bb,quantreg=T)
```

DHARMA residual diagnostics



```
testDispersion(sim_mod_seedpred_bb)
```

**DHARMA nonparametric dispersion test via sd of
residuals fitted vs. simulated**



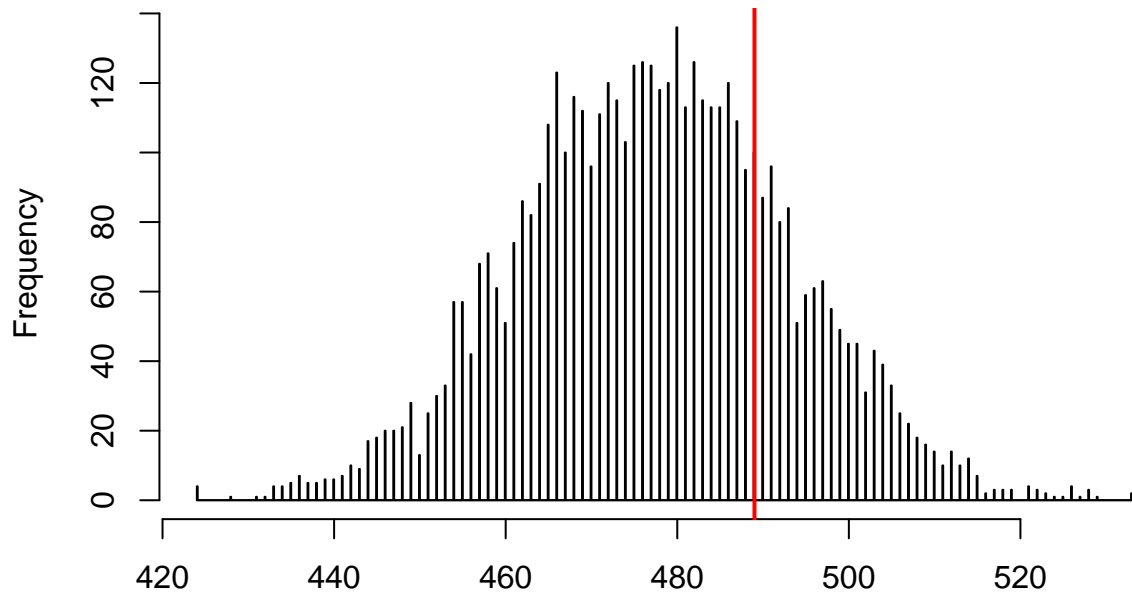
Simulated values, red line = fitted model. p-value (two.sided) = 0.0024

```
##  
## DHARMA nonparametric dispersion test via sd of residuals fitted vs.  
## simulated  
##  
## data: simulationOutput  
## ratioObsSim = 0.85972, p-value = 0.0024  
## alternative hypothesis: two.sided
```

Slight underdispersion.

```
testZeroInflation(sim_mod_seedpred_bb)
```

**DHARMA zero-inflation test via comparison to
expected zeros with simulation under H0 = fitted
model**



Simulated values, red line = fitted model. p-value (two.sided) = 0.4808

```
##
## DHARMA zero-inflation test via comparison to expected zeros with
## simulation under H0 = fitted model
##
## data: simulationOutput
## ratioObsSim = 1.0244, p-value = 0.4808
## alternative hypothesis: two.sided
```

OK.

```
anova(mod_seedpred,mod_seedpred_bb)
```

```
## Data: subset(data_selag, n_seeds > 0)
## Models:
## mod_seedpred: cbind(round(n_pred_seeds), round(n_intact_seeds)) ~ (scale(mean_3) + , zi=~0, disp=~1
## mod_seedpred:      scale(mean_4) + scale(mean_5) + scale(mean_6)) * FFD_s_y + , zi=~0, disp=~1
## mod_seedpred:      n_fl_s_y + (1 | id), zi=~0, disp=~1
## mod_seedpred_bb: cbind(round(n_pred_seeds), round(n_intact_seeds)) ~ (scale(mean_3) + , zi=~0, disp=
## mod_seedpred_bb:      scale(mean_4) + scale(mean_5) + scale(mean_6)) * FFD_s_y + , zi=~0, disp=~1
## mod_seedpred_bb:      n_fl_s_y + (1 | id), zi=~0, disp=~1
##
##           Df      AIC      BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
## mod_seedpred   12 9018.9 9080.7 -4497.4   8994.9
## mod_seedpred_bb 13 5339.2 5406.3 -2656.6   5313.2 3681.6      1 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```