RESULTS FROM FIELD DATA 2015 – 23/02/2016

Butterfly seed predation: effects on plant reproductive output and context-dependence

Objectives / questions

1) What are the effects of plant traits (phenology, flower production, shoot height), environmental context (soil temperature, height of surrounding vegetation) and community context (ant abundance at the plant level, distance to nearest plant with ants) on predispersal seed predation (probability of attack, intensity)?

H1: Plants are more prone to be attacked by the butterfly (and the interaction is more intense) when they show an early phenology, high number of flowers and higher shoots, when the surrounding vegetation is short and when ants are present in the proximity of the plant. Reasons for an effect of soil temperature?

2) What are the (direct / indirect) effects of plant traits and context on fitness / reproductive output (fruit / seed production) / (fruit / seed set)?

H2: Higher soil temperatures (speeding up fruit maturation?) and higher flower production directly increase fitness. The effects of phenology, height and ants are indirect effects through seed predation (plants flowering early, being higher than the surrounding vegetation and having high ant abundance have higher seed predation and therefore lower fitness).

3) What is the relative importance of plant traits vs. context for explaining the variation in predispersal seed predation? What is the relative importance of plant traits, context and seed predation for explaining the variation in plant fitness / reproductive output? (variation partitioning)

H3: … We could hypothesize that the context is (nearly) as important as plant traits for explaining variation in seed predation, and that the interaction is (nearly) as important as plant traits for explaining variation in fitness / reproductive output.

…

1) Effects of plant traits, environmental and community context on seed predation

First constructed a model (GLM) including the interactions of all variables \* population (results not shown), then a model were only the significant interactions were kept. Explanatory variables were standardized before including them in the model (z.) in order to improve the interpretation of model coefficients.

Model for probability of attack, n=301

> summary(model2b)

Call:

glm(formula = attack ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + population + population:z.veg\_h\_mean, family = "binomial",

na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-3.4223 -0.8454 0.3245 0.7332 2.4499

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 1.96068 0.38328 5.116 3.13e-07 \*\*\*

z.shoot\_h 0.53144 0.21741 2.444 0.014507 \*

z.veg\_h\_mean -1.33414 0.36116 -3.694 0.000221 \*\*\*

z.most\_adv 0.78995 0.24505 3.224 0.001266 \*\*

z.n\_fl\_corrected 0.75712 0.32137 2.356 0.018478 \*

z.n\_redants 0.22181 0.17497 1.268 0.204921

z.dist\_closest\_redants -0.12831 0.16525 -0.776 0.437474

z.avg\_d\_min\_ja -1.29483 0.26479 -4.890 1.01e-06 \*\*\*

populationRemmene -1.84709 0.57704 -3.201 0.001370 \*\*

populationTånga Hed -1.72450 0.65242 -2.643 0.008212 \*\*

z.veg\_h\_mean:populationRemmene 0.02117 0.45736 0.046 0.963074

z.veg\_h\_mean:populationTånga Hed 0.97211 0.52284 1.859 0.062988 .

---

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 405.63 on 300 degrees of freedom

Residual deviance: 289.59 on 289 degrees of freedom

AIC: 313.59

Number of Fisher Scoring iterations: 5

> Anova(model2b,type="II")

Analysis of Deviance Table (Type II tests)

Response: attack

LR Chisq Df Pr(>Chisq)

z.shoot\_h 6.2236 1 0.0126057 \*

z.veg\_h\_mean 23.3334 1 1.362e-06 \*\*\*

z.most\_adv 11.2901 1 0.0007792 \*\*\*

z.n\_fl\_corrected 6.1794 1 0.0129245 \*

z.n\_redants 1.6501 1 0.1989424

z.dist\_closest\_redants 0.6120 1 0.4340289

z.avg\_d\_min\_ja 30.6549 1 3.082e-08 \*\*\*

population 17.7083 2 0.0001428 \*\*\*

z.veg\_h\_mean:population 4.4713 2 0.1069208

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> r.squaredLR(model2b)

[1] 0.3199009

attr(,"adj.r.squared")

[1] 0.4322151

According to this model, the probability of attack increases with shoot height and decreases with height of the surrounding vegetation (tested the interaction but it was not significant). It also increases with early flowering and with number of flowers, and decreases with soil temperature (why??). There is no effect of *Myrmica* abundance or distance to closest plant with ants. There is also a significant effect of population on probability of attack.

Graphs showing the change in response of attack to veg\_h\_mean for each population, holding all other variables constant (median)



Model for n\_eggs\_max n=301

> summary(model2eg\_b)

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

Family: poisson ( log )

Formula: n\_eggs\_max ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv + z.n\_fl\_corrected +

z.n\_redants + z.dist\_closest\_redants + z.avg\_d\_min\_ja + population +

population:z.veg\_h\_mean + population:z.n\_redants + population:z.dist\_closest\_redants + (1 | id)

Control: glmerControl(optimizer = "bobyqa")

AIC BIC logLik deviance df.resid

1403.1 1466.1 -684.6 1369.1 284

Scaled residuals:

Min 1Q Median 3Q Max

-1.5065 -0.5905 -0.1132 0.2491 1.7780

Random effects:

Groups Name Variance Std.Dev.

id (Intercept) 1.29 1.136

Number of obs: 301, groups: id, 301

Fixed effects:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 1.35203 0.19753 6.845 7.66e-12 \*\*\*

z.shoot\_h 0.40681 0.12257 3.319 0.000904 \*\*\*

z.veg\_h\_mean -0.89158 0.23348 -3.819 0.000134 \*\*\*

z.most\_adv 0.66453 0.13018 5.105 3.31e-07 \*\*\*

z.n\_fl\_corrected 0.39176 0.13951 2.808 0.004983 \*\*

z.n\_redants 0.49917 0.18478 2.701 0.006905 \*\*

z.dist\_closest\_redants -0.28038 0.29967 -0.936 0.349461

z.avg\_d\_min\_ja -0.74566 0.13092 -5.696 1.23e-08 \*\*\*

populationRemmene -0.54385 0.35959 -1.512 0.130424

populationTånga Hed -1.15740 0.34808 -3.325 0.000884 \*\*\*

z.veg\_h\_mean:populationRemmene 0.18273 0.28405 0.643 0.520027

z.veg\_h\_mean:populationTånga Hed 0.72644 0.29841 2.434 0.014918 \*

z.n\_redants:populationRemmene 0.02762 0.42636 0.065 0.948356

z.n\_redants:populationTånga Hed -0.39263 0.21102 -1.861 0.062789 .

z.dist\_closest\_redants:populationRemmene 1.74673 0.56176 3.109 0.001875 \*\*

z.dist\_closest\_redants:populationTånga Hed 0.22722 0.31383 0.724 0.469056

---

> Anova(model2eg\_b)

Analysis of Deviance Table (Type II Wald chisquare tests)

Response: n\_eggs\_max

Chisq Df Pr(>Chisq)

z.shoot\_h 11.0154 1 0.0009036 \*\*\*

z.veg\_h\_mean 16.8416 1 4.063e-05 \*\*\*

z.most\_adv 26.0582 1 3.313e-07 \*\*\*

z.n\_fl\_corrected 7.8856 1 0.0049831 \*\*

z.n\_redants 6.1037 1 0.0134897 \*

z.dist\_closest\_redants 0.0920 1 0.7616433

z.avg\_d\_min\_ja 32.4401 1 1.229e-08 \*\*\*

population 20.1820 2 4.145e-05 \*\*\*

z.veg\_h\_mean:population 6.7727 2 0.0338321 \*

z.n\_redants:population 4.1815 2 0.1235922

z.dist\_closest\_redants:population 10.5952 2 0.0050037 \*\*

---

> r.squaredLR(model2eg\_b,null.RE=T) #R squared for fixed factors

[1] 0.4237756

attr(,"adj.r.squared")

[1] 0.4263757

The same variables that increase probability of attack increase also interaction intensity measured as number of eggs per plant, but in this case the effect of the height of the surrounding vegetation differs among populations, and interaction intensity also increases with ant abundance in all populations (interaction with population not significant). There is an effect of distance to the closest plant with ants which differs among populations.

Graphs showing the change in response of attack to veg\_h\_mean, n\_redants and dist\_closest\_redants for each population, holding all other variables constant (median)

Model for prop\_predated (fruits, flowers and buds) n =301



> summary(model2pred\_prop\_b)

Call:

glm(formula = prop\_pred ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + population, family = "binomial", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-3.2006 -0.8414 -0.3896 0.4293 2.4597

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.86283 0.15342 -5.624 1.86e-08 \*\*\*

z.shoot\_h 0.25743 0.08322 3.094 0.001978 \*\*

z.veg\_h\_mean -0.18101 0.09605 -1.885 0.059487 .

z.most\_adv 0.42783 0.09326 4.587 4.49e-06 \*\*\*

z.n\_fl\_corrected -0.11700 0.08339 -1.403 0.160609

z.n\_redants 0.05060 0.05994 0.844 0.398536

z.dist\_closest\_redants 0.02488 0.05157 0.482 0.629533

z.avg\_d\_min\_ja -0.31315 0.10282 -3.046 0.002322 \*\*

populationRemmene -0.50207 0.24177 -2.077 0.037832 \*

populationTånga Hed -0.92847 0.25866 -3.590 0.000331 \*\*\*

---

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 295.98 on 300 degrees of freedom

Residual deviance: 247.71 on 291 degrees of freedom

AIC: 642.03

Number of Fisher Scoring iterations: 4

> Anova(model2pred\_prop\_b)

Analysis of Deviance Table (Type II tests)

Response: prop\_pred

LR Chisq Df Pr(>Chisq)

z.shoot\_h 9.5754 1 0.001972 \*\*

z.veg\_h\_mean 3.6493 1 0.056093 .

z.most\_adv 21.4098 1 3.709e-06 \*\*\*

z.n\_fl\_corrected 1.9795 1 0.159442

z.n\_redants 0.7012 1 0.402392

z.dist\_closest\_redants 0.2304 1 0.631234

z.avg\_d\_min\_ja 9.1802 1 0.002447 \*\*

population 13.1352 2 0.001405 \*\*

---

> r.squaredLR(model2pred\_prop\_b)

[1] 0.1481604

attr(,"adj.r.squared")

[1] 0.1660731

According to this model, interaction intensity measured as proportion of predated fruits, flowers and buds increases with shoot height, with early flowering and with number of flowers, and decreases with soil temperature. Interaction intensity differs significantly among populations.

2) Effects of plant traits, environmental and community context on fitness / reproductive output

Same procedure: first constructed a model including the interactions of all variables \* population (results not shown), then a model were only the significant interactions were kept.

Explanatory variables were standardized before including them in the model (z.) in order to improve the interpretation of model coefficients.

First, number of intact fruits was used as a measure of fitness (although I did not perform classic selection analyses – i.e. fitness is not relativized – so better call it reproductive output?). I also run models with fruit set as a response variable because I thought that could be also interesting (as that would depend less on traits, for example on the number of flowers).

Then, I used number of developed seeds (per plant – well, per marked shoot). A problem here is that many plants did not produce any fruit, so seed number is zero on those. Poisson distribution does not really work well here because the data are both overdispersed and with many zeros, so I tried a zero-inflation model (I think it is also interesting to see which factors explain the production of zero seeds = no fruit production, and the production of different amounts of seeds). For those models I used only plants from where I had complete seed information (either I have number of seeds in intact and predated fruits, if any, or plants produced no fruits).

n plants where information on seeds is available (many with n fruits = 0)

population n plants n plants with >0 seeds prop plants >0 seeds

Högsjön 96 26 0,27083333

Remmene 84 8 0,0952381

Tånga Hed 71 60 0,84507042

After removal of some plants with missing data for temperature and two outliers, n=244 plants (93 Högsjön, 82 Remmene, 69 Tanga).

I included the interaction with the seed predator in the models in three ways, as measured before: probability of attack, number of eggs per plant and proportion of predated fruits, flowers and seeds.

2.1) Response = n\_intact\_fruits

interaction = attack

> summary(model1fr\_b)

Call:

glm(formula = n\_intact\_fruits ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.dist\_closest\_redants + z.avg\_d\_min\_ja + attack + population +

population:z.veg\_h\_mean, family = "poisson", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-2.6892 -0.7339 -0.5232 0.5054 2.4252

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.83688 0.22793 -3.672 0.000241 \*\*\*

z.shoot\_h 0.13260 0.08038 1.650 0.098999 .

z.veg\_h\_mean -0.21728 0.20678 -1.051 0.293366

z.most\_adv 0.04058 0.08434 0.481 0.630458

z.n\_fl\_corrected 0.30552 0.06737 4.535 5.77e-06 \*\*\*

z.n\_redants -0.03755 0.04899 -0.766 0.443387

z.dist\_closest\_redants -0.01652 0.03807 -0.434 0.664276

z.avg\_d\_min\_ja 0.27649 0.11814 2.340 0.019268 \*

attack1 -0.46097 0.12685 -3.634 0.000279 \*\*\*

populationRemmene -0.38068 0.38293 -0.994 0.320152

populationTånga Hed 1.68251 0.25714 6.543 6.02e-11 \*\*\*

z.veg\_h\_mean:populationRemmene 0.50758 0.23804 2.132 0.032976 \*

z.veg\_h\_mean:populationTånga Hed 0.12082 0.22339 0.541 0.588601

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(Dispersion parameter for poisson family taken to be 1)

Null deviance: 764.28 on 300 degrees of freedom

Residual deviance: 258.69 on 288 degrees of freedom

AIC: 646.22

Number of Fisher Scoring iterations: 6

> Anova(model1fr\_b)

Analysis of Deviance Table (Type II tests)

Response: n\_intact\_fruits

LR Chisq Df Pr(>Chisq)

z.shoot\_h 2.698 1 0.1005011

z.veg\_h\_mean 0.065 1 0.7986506

z.most\_adv 0.231 1 0.6306370

z.n\_fl\_corrected 20.295 1 6.639e-06 \*\*\*

z.n\_redants 0.601 1 0.4381981

z.dist\_closest\_redants 0.190 1 0.6625540

z.avg\_d\_min\_ja 5.705 1 0.0169146 \*

attack 12.668 1 0.0003719 \*\*\*

population 75.098 2 < 2.2e-16 \*\*\*

z.veg\_h\_mean:population 6.115 2 0.0469993 \*

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> r.squaredLR(model1fr\_b)

[1] 0.8135703

attr(,"adj.r.squared")

[1] 0.8333616

According to this model, flower production increases fitness, which also increases with soil temperature and decreases with butterfly attack. There is an effect of height of the surrounding vegetation which varies among populations (see graphs below), and there are also important differences in fitness among populations.



interaction = n\_eggs

> summary(model1fr\_b)

Call:

glm(formula = n\_intact\_fruits ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + z.n\_eggs\_max + population + population:z.veg\_h\_mean,

family = "poisson", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-1.9855 -0.7282 -0.4730 0.3519 2.3261

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.997080 0.214870 -4.640 3.48e-06 \*\*\*

z.shoot\_h 0.251883 0.080685 3.122 0.0018 \*\*

z.veg\_h\_mean -0.264523 0.208787 -1.267 0.2052

z.most\_adv 0.174045 0.088184 1.974 0.0484 \*

z.n\_fl\_corrected 0.354160 0.066613 5.317 1.06e-07 \*\*\*

z.n\_redants -0.032759 0.051883 -0.631 0.5278

z.dist\_closest\_redants 0.006916 0.039178 0.177 0.8599

z.avg\_d\_min\_ja 0.228762 0.117313 1.950 0.0512 .

z.n\_eggs\_max -0.423368 0.060617 -6.984 2.86e-12 \*\*\*

populationRemmene -0.542560 0.387604 -1.400 0.1616

populationTånga Hed 1.323504 0.269775 4.906 9.30e-07 \*\*\*

z.veg\_h\_mean:populationRemmene 0.562590 0.243052 2.315 0.0206 \*

z.veg\_h\_mean:populationTånga Hed 0.066158 0.228980 0.289 0.7726

---

(Dispersion parameter for poisson family taken to be 1)

Null deviance: 764.28 on 300 degrees of freedom

Residual deviance: 213.06 on 288 degrees of freedom

AIC: 600.58

Number of Fisher Scoring iterations: 6

> Anova(model1fr\_b)

Analysis of Deviance Table (Type II tests)

Response: n\_intact\_fruits

LR Chisq Df Pr(>Chisq)

z.shoot\_h 9.586 1 0.001961 \*\*

z.veg\_h\_mean 1.146 1 0.284333

z.most\_adv 3.895 1 0.048440 \*

z.n\_fl\_corrected 27.687 1 1.426e-07 \*\*\*

z.n\_redants 0.407 1 0.523426

z.dist\_closest\_redants 0.031 1 0.860158

z.avg\_d\_min\_ja 3.943 1 0.047070 \*

z.n\_eggs\_max 58.302 1 2.248e-14 \*\*\*

population 50.480 2 1.093e-11 \*\*\*

z.veg\_h\_mean:population 7.891 2 0.019340 \*

---

> r.squaredLR(model1fr\_b)

[1] 0.839796

attr(,"adj.r.squared")

[1] 0.8602252

Results of this model are very similar to the previous one, but there are also significant positive effects of shoot height and early phenology on fitness. Interaction intensity has in this case the strongest effect on fitness.



interaction = prop\_predated

> summary(model1fr\_b)

Call:

glm(formula = n\_intact\_fruits ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + scale(prop\_pred\_num) + population, family = "poisson",

na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-2.3721 -0.7187 -0.4656 0.4138 2.2121

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -1.13977 0.20658 -5.517 3.44e-08 \*\*\*

z.shoot\_h 0.22103 0.07812 2.829 0.004665 \*\*

z.veg\_h\_mean -0.08514 0.08490 -1.003 0.315908

z.most\_adv 0.22945 0.09054 2.534 0.011268 \*

z.n\_fl\_corrected 0.22273 0.06747 3.301 0.000963 \*\*\*

z.n\_redants -0.04514 0.04989 -0.905 0.365650

z.dist\_closest\_redants 0.01442 0.03899 0.370 0.711480

z.avg\_d\_min\_ja 0.16819 0.12158 1.383 0.166550

scale(prop\_pred\_num) -0.62953 0.08531 -7.379 1.59e-13 \*\*\*

populationRemmene -0.25414 0.35936 -0.707 0.479451

populationTånga Hed 1.41912 0.26311 5.394 6.90e-08 \*\*\*

---

(Dispersion parameter for poisson family taken to be 1)

Null deviance: 764.28 on 300 degrees of freedom

Residual deviance: 215.93 on 290 degrees of freedom

AIC: 599.46

Number of Fisher Scoring iterations: 5

> Anova(model1fr\_b)

Analysis of Deviance Table (Type II tests)

Response: n\_intact\_fruits

LR Chisq Df Pr(>Chisq)

z.shoot\_h 7.834 1 0.005126 \*\*

z.veg\_h\_mean 1.030 1 0.310244

z.most\_adv 6.412 1 0.011336 \*

z.n\_fl\_corrected 10.757 1 0.001039 \*\*

z.n\_redants 0.843 1 0.358655

z.dist\_closest\_redants 0.136 1 0.712645

z.avg\_d\_min\_ja 1.955 1 0.161997

scale(prop\_pred\_num) 61.631 1 4.143e-15 \*\*\*

population 45.123 2 1.591e-10 \*\*\*

---

> r.squaredLR(model1fr\_b)

[1] 0.8382602

attr(,"adj.r.squared")

[1] 0.858652

Results are similar to the previous model, but there is no effect of soil temperature.

2.2) Response = fruit\_set

interaction = attack

> summary(model1frs\_b)

Call:

glm(formula = fruit\_set1 ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + attack + population + population:z.n\_fl\_corrected,

family = "binomial", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-2.3443 -0.7508 -0.4753 0.3880 2.6921

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -2.29699 0.32015 -7.175 7.25e-13 \*\*\*

z.shoot\_h 0.20687 0.08483 2.439 0.01474 \*

z.veg\_h\_mean -0.02116 0.08854 -0.239 0.81115

z.most\_adv 0.16142 0.09140 1.766 0.07738 .

z.n\_fl\_corrected -1.31030 0.45366 -2.888 0.00387 \*\*

z.n\_redants -0.09465 0.05424 -1.745 0.08097 .

z.dist\_closest\_redants -0.03519 0.04218 -0.834 0.40415

z.avg\_d\_min\_ja 0.30506 0.12605 2.420 0.01551 \*

attack1 -0.43991 0.14469 -3.040 0.00236 \*\*

populationRemmene 0.83082 0.38999 2.130 0.03314 \*

populationTånga Hed 1.87893 0.35034 5.363 8.18e-08 \*\*\*

z.n\_fl\_corrected:populationRemmene 1.36628 0.49436 2.764 0.00571 \*\*

z.n\_fl\_corrected:populationTånga Hed 1.17710 0.44972 2.617 0.00886 \*\*

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(Dispersion parameter for binomial family taken to be 1)

Null deviance: 366.68 on 300 degrees of freedom

Residual deviance: 206.50 on 288 degrees of freedom

AIC: 589.91

Number of Fisher Scoring iterations: 5

> Anova(model1frs\_b)

Analysis of Deviance Table (Type II tests)

Response: fruit\_set1

LR Chisq Df Pr(>Chisq)

z.shoot\_h 5.948 1 0.014738 \*

z.veg\_h\_mean 0.057 1 0.810851

z.most\_adv 3.118 1 0.077424 .

z.n\_fl\_corrected 3.250 1 0.071442 .

z.n\_redants 3.130 1 0.076859 .

z.dist\_closest\_redants 0.701 1 0.402606

z.avg\_d\_min\_ja 6.051 1 0.013897 \*

attack 9.195 1 0.002427 \*\*

population 31.717 2 1.297e-07 \*\*\*

z.n\_fl\_corrected:population 9.979 2 0.006809 \*\*

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> r.squaredLR(model1frs\_b)

[1] 0.4126504

attr(,"adj.r.squared")

[1] 0.4535679

#Error making graphs

According to this model, fruit set increases with shoot height and soil temperature and decreases with butterfly attack. There are differences among populations in fruit set and in the effect of flower production on fruit set.

interaction = n\_eggs

> summary(model1frs\_b)

Call:

glm(formula = fruit\_set1 ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + population + z.n\_eggs\_max + population:z.n\_fl\_corrected,

family = "binomial", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-2.2145 -0.7495 -0.4141 0.3949 2.0955

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -2.51979 0.30565 -8.244 < 2e-16 \*\*\*

z.shoot\_h 0.27144 0.08681 3.127 0.00177 \*\*

z.veg\_h\_mean -0.04716 0.09117 -0.517 0.60497

z.most\_adv 0.22909 0.09349 2.451 0.01427 \*

z.n\_fl\_corrected -1.38617 0.45571 -3.042 0.00235 \*\*

z.n\_redants -0.08926 0.05533 -1.613 0.10674

z.dist\_closest\_redants -0.01215 0.04211 -0.288 0.77299

z.avg\_d\_min\_ja 0.28808 0.12515 2.302 0.02135 \*

populationRemmene 0.75185 0.39255 1.915 0.05545 .

populationTånga Hed 1.66815 0.35687 4.674 2.95e-06 \*\*\*

z.n\_eggs\_max -0.25794 0.05501 -4.689 2.74e-06 \*\*\*

z.n\_fl\_corrected:populationRemmene 1.53510 0.50554 3.037 0.00239 \*\*

z.n\_fl\_corrected:populationTånga Hed 1.31080 0.45271 2.895 0.00379 \*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 366.68 on 300 degrees of freedom

Residual deviance: 192.72 on 288 degrees of freedom

AIC: 576.12

Number of Fisher Scoring iterations: 5

> Anova(model1frs\_b)

Analysis of Deviance Table (Type II tests)

Response: fruit\_set1

LR Chisq Df Pr(>Chisq)

z.shoot\_h 9.7863 1 0.001758 \*\*

z.veg\_h\_mean 0.2697 1 0.603504

z.most\_adv 6.0200 1 0.014145 \*

z.n\_fl\_corrected 1.1477 1 0.284038

z.n\_redants 2.6736 1 0.102022

z.dist\_closest\_redants 0.0834 1 0.772747

z.avg\_d\_min\_ja 5.4707 1 0.019338 \*

population 20.8320 2 2.995e-05 \*\*\*

z.n\_eggs\_max 22.9813 1 1.636e-06 \*\*\*

z.n\_fl\_corrected:population 12.5943 2 0.001842 \*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> r.squaredLR(model1frs\_b)

[1] 0.4389461

attr(,"adj.r.squared")

[1] 0.482471

#Error making graphs

This model shows similar effects as the previous one plus a positive effect of early flowering on fruit set. Interaction intensity has the strongest effect on fitness.

interaction = prop\_predated

> summary(model1frs\_b)

Call:

glm(formula = fruit\_set1 ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants +

z.avg\_d\_min\_ja + z.n\_fl\_corrected \* population + scale(prop\_pred\_num),

family = "binomial", na.action = "na.fail")

Deviance Residuals:

Min 1Q Median 3Q Max

-2.3961 -0.7614 -0.4491 0.4083 2.9162

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -2.54883 0.30136 -8.458 < 2e-16 \*\*\*

z.shoot\_h 0.23189 0.08671 2.674 0.00749 \*\*

z.veg\_h\_mean -0.01991 0.08835 -0.225 0.82171

z.most\_adv 0.19984 0.09692 2.062 0.03921 \*

z.n\_fl\_corrected -1.45864 0.44497 -3.278 0.00105 \*\*

z.n\_redants -0.09554 0.05416 -1.764 0.07773 .

z.dist\_closest\_redants -0.01219 0.04173 -0.292 0.77011

z.avg\_d\_min\_ja 0.30606 0.12638 2.422 0.01544 \*

populationRemmene 0.83278 0.38895 2.141 0.03226 \*

populationTånga Hed 1.74546 0.35290 4.946 7.57e-07 \*\*\*

scale(prop\_pred\_num) -0.21700 0.08043 -2.698 0.00698 \*\*

z.n\_fl\_corrected:populationRemmene 1.43855 0.48769 2.950 0.00318 \*\*

z.n\_fl\_corrected:populationTånga Hed 1.29186 0.44125 2.928 0.00341 \*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 366.68 on 300 degrees of freedom

Residual deviance: 208.24 on 288 degrees of freedom

AIC: 591.65

Number of Fisher Scoring iterations: 5

> Anova(model1frs\_b)

Analysis of Deviance Table (Type II tests)

Response: fruit\_set1

LR Chisq Df Pr(>Chisq)

z.shoot\_h 7.1532 1 0.007483 \*\*

z.veg\_h\_mean 0.0509 1 0.821449

z.most\_adv 4.2654 1 0.038896 \*

z.n\_fl\_corrected 5.2382 1 0.022096 \*

z.n\_redants 3.1988 1 0.073691 .

z.dist\_closest\_redants 0.0856 1 0.769877

z.avg\_d\_min\_ja 6.0578 1 0.013845 \*

population 24.2767 2 5.35e-06 \*\*\*

scale(prop\_pred\_num) 7.4551 1 0.006326 \*\*

z.n\_fl\_corrected:population 12.3384 2 0.002093 \*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> r.squaredLR(model1frs\_b)

[1] 0.4092462

attr(,"adj.r.squared")

[1] 0.4498261

This model shows similar effects as the previous one but now the effect of population is the strongest.

2.3) Response = seed\_n\_per\_shoot

interaction = attack

Using glmer, poisson distribution

> summary(model1se\_b)

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

Family: poisson ( log )

Formula: round(seed\_n\_per\_shoot) ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants + z.avg\_d\_min\_ja + attack + population + (1 | id)

Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))

AIC BIC logLik deviance df.resid

1899.4 1941.4 -937.7 1875.4 232

Scaled residuals:

Min 1Q Median 3Q Max

-0.51621 -0.09910 -0.02609 0.00135 0.11084

Random effects:

Groups Name Variance Std.Dev.

id (Intercept) 27.61 5.254

Number of obs: 244, groups: id, 244

Fixed effects:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -1.6342 1.2468 -1.311 0.1899

z.shoot\_h 1.1827 0.5701 2.074 0.0380 \*

z.veg\_h\_mean -0.1939 0.4999 -0.388 0.6981

z.most\_adv 1.3307 0.6225 2.138 0.0325 \*

z.n\_fl\_corrected 0.4663 0.6530 0.714 0.4751

z.n\_redants -0.2113 0.3972 -0.532 0.5947

z.dist\_closest\_redants 0.1634 0.3833 0.426 0.6699

z.avg\_d\_min\_ja 1.2607 0.6675 1.889 0.0589 .

attack1 -2.8299 1.0012 -2.827 0.0047 \*\*

populationRemmene -1.0685 1.3629 -0.784 0.4330

populationTånga Hed 6.4151 1.5269 4.201 2.65e-05 \*\*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> Anova(model1se\_b)

Analysis of Deviance Table (Type II Wald chisquare tests)

Response: round(seed\_n\_per\_shoot)

Chisq Df Pr(>Chisq)

z.shoot\_h 4.3029 1 0.038047 \*

z.veg\_h\_mean 0.1505 1 0.698078

z.most\_adv 4.5703 1 0.032531 \*

z.n\_fl\_corrected 0.5100 1 0.475147

z.n\_redants 0.2830 1 0.594727

z.dist\_closest\_redants 0.1817 1 0.669893

z.avg\_d\_min\_ja 3.5669 1 0.058943 .

attack 7.9897 1 0.004704 \*\*

population 25.0012 2 3.724e-06 \*\*\*

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> r.squaredLR(model1se\_b,null.RE=T)

[1] 0.3770115

attr(,"adj.r.squared")

[1] 0.3771194

Graph of residuals



interaction = attack

Using zero-inflated, negative binomial (Not including interactions with population)

> summary(model1se\_c)

Call:

zeroinfl(formula = round(seed\_n\_per\_shoot) ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv + z.n\_fl\_corrected +

z.n\_redants + z.dist\_closest\_redants + z.avg\_d\_min\_ja + attack + population, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max

-1.243322 -0.412709 -0.222756 0.008336 5.285480

Count model coefficients (negbin with log link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) 5.770917 0.214266 26.933 < 2e-16 \*\*\*

z.shoot\_h 0.143255 0.104778 1.367 0.1716

z.veg\_h\_mean -0.043917 0.084126 -0.522 0.6016

z.most\_adv 0.075734 0.119438 0.634 0.5260

z.n\_fl\_corrected 0.255486 0.116321 2.196 0.0281 \*

z.n\_redants -0.005496 0.066497 -0.083 0.9341

z.dist\_closest\_redants 0.024459 0.058162 0.421 0.6741

z.avg\_d\_min\_ja -0.005871 0.124013 -0.047 0.9622

attack1 -0.412537 0.187784 -2.197 0.0280 \*

populationRemmene 0.580758 0.376033 1.544 0.1225

populationTånga Hed 1.732704 0.280630 6.174 6.64e-10 \*\*\*

Log(theta) 0.754059 0.140474 5.368 7.96e-08 \*\*\*

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.02354 0.49362 -0.048 0.96196

z.shoot\_h -0.43467 0.28155 -1.544 0.12262

z.veg\_h\_mean 0.11241 0.25510 0.441 0.65947

z.most\_adv -0.67203 0.30311 -2.217 0.02661 \*

z.n\_fl\_corrected -0.58694 0.38498 -1.525 0.12736

z.n\_redants 0.20267 0.19385 1.046 0.29578

z.dist\_closest\_redants -0.30232 0.29056 -1.040 0.29811

z.avg\_d\_min\_ja -0.52861 0.29460 -1.794 0.07276 .

attack1 1.59391 0.49712 3.206 0.00134 \*\*

populationRemmene 0.79095 0.68784 1.150 0.25019

populationTånga Hed -1.64007 0.67468 -2.431 0.01506 \*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Theta = 2.1256

Number of iterations in BFGS optimization: 40

Log-likelihood: -811.1 on 23 Df

> r.squaredLR(model1se\_c)

[1] 0.622944

attr(,"adj.r.squared")

[1] 0.6232486

interaction = n\_eggs - Using zero-inflated, negative binomial

> summary(model2se\_d)

Call:

zeroinfl(formula = round(seed\_n\_per\_shoot) ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv + z.n\_fl\_corrected +

z.avg\_d\_min\_ja + z.n\_eggs\_max + population + z.n\_redants + z.dist\_closest\_redants +

population:z.most\_adv + population:z.avg\_d\_min\_ja | z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.avg\_d\_min\_ja + z.n\_eggs\_max + population + z.n\_redants + z.dist\_closest\_redants +

population:z.n\_fl\_corrected, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max

-1.35034 -0.43662 -0.17817 0.07955 5.38187

Count model coefficients (negbin with log link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) 6.02201 0.29435 20.459 < 2e-16 \*\*\*

z.shoot\_h 0.06137 0.10395 0.590 0.554894

z.veg\_h\_mean 0.03423 0.08426 0.406 0.684562

z.most\_adv 0.95484 0.37757 2.529 0.011442 \*

z.n\_fl\_corrected 0.44107 0.12720 3.467 0.000525 \*\*\*

z.avg\_d\_min\_ja -0.10928 0.16552 -0.660 0.509095

z.n\_eggs\_max -0.33365 0.09261 -3.603 0.000315 \*\*\*

populationRemmene -0.50863 0.61637 -0.825 0.409256

populationTånga Hed 1.01607 0.38226 2.658 0.007859 \*\*

z.n\_redants 0.02258 0.06122 0.369 0.712278

z.dist\_closest\_redants 0.01176 0.05634 0.209 0.834643

z.most\_adv:populationRemmene -1.16585 0.43379 -2.688 0.007197 \*\*

z.most\_adv:populationTånga Hed -0.82955 0.40073 -2.070 0.038446 \*

z.avg\_d\_min\_ja:populationRemmene -0.50946 0.56652 -0.899 0.368506

z.avg\_d\_min\_ja:populationTånga Hed 0.14910 0.27324 0.546 0.585291

Log(theta) 0.90023 0.14228 6.327 2.5e-10 \*\*\*

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) 1.42829 0.45729 3.123 0.001788 \*\*

z.shoot\_h -0.53488 0.29131 -1.836 0.066342 .

z.veg\_h\_mean 0.01173 0.24768 0.047 0.962221

z.most\_adv -0.70647 0.31798 -2.222 0.026300 \*

z.n\_fl\_corrected -0.07229 0.61758 -0.117 0.906818

z.avg\_d\_min\_ja -0.63954 0.28750 -2.225 0.026114 \*

z.n\_eggs\_max 1.44294 0.37948 3.802 0.000143 \*\*\*

populationRemmene 0.34419 0.75893 0.454 0.650173

populationTånga Hed -1.52449 0.74512 -2.046 0.040761 \*

z.n\_redants 0.17618 0.19652 0.897 0.369980

z.dist\_closest\_redants -0.20034 0.30190 -0.664 0.506945

z.n\_fl\_corrected:populationRemmene -0.78920 0.84147 -0.938 0.348310

z.n\_fl\_corrected:populationTånga Hed -2.04645 0.85990 -2.380 0.017318 \*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Theta = 2.4602

Number of iterations in BFGS optimization: 36

Log-likelihood: -796.5 on 29 Df

> r.squaredLR(model2se\_d)

[1] 0.6656435

attr(,"adj.r.squared")

[1] 0.6659689

interaction = n\_predated - Using zero-inflated, negative binomial

> summary(model3se\_d)

Call:

zeroinfl(formula = round(seed\_n\_per\_shoot) ~ z.shoot\_h + z.veg\_h\_mean + z.most\_adv + z.n\_fl\_corrected +

z.n\_redants + z.dist\_closest\_redants + z.avg\_d\_min\_ja + scale(prop\_pred\_num) + population +

population:z.most\_adv + population:z.veg\_h\_mean | z.shoot\_h + z.veg\_h\_mean + z.most\_adv +

z.n\_fl\_corrected + z.n\_redants + z.dist\_closest\_redants + z.avg\_d\_min\_ja + scale(prop\_pred\_num),

dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max

-1.30940 -0.44530 -0.23110 0.01481 6.65961

Count model coefficients (negbin with log link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) 6.030893 0.273398 22.059 < 2e-16 \*\*\*

z.shoot\_h 0.046816 0.107724 0.435 0.663856

z.veg\_h\_mean 0.307025 0.135628 2.264 0.023591 \*

z.most\_adv 1.380043 0.407052 3.390 0.000698 \*\*\*

z.n\_fl\_corrected 0.246538 0.110667 2.228 0.025897 \*

z.n\_redants -0.005175 0.064672 -0.080 0.936226

z.dist\_closest\_redants 0.051130 0.057916 0.883 0.377327

z.avg\_d\_min\_ja 0.024883 0.131099 0.190 0.849464

scale(prop\_pred\_num) -0.150903 0.104608 -1.443 0.149146

populationRemmene 0.630840 0.519372 1.215 0.224511

populationTånga Hed 1.139673 0.357607 3.187 0.001438 \*\*

z.most\_adv:populationRemmene -1.663981 0.490844 -3.390 0.000699 \*\*\*

z.most\_adv:populationTånga Hed -1.307293 0.419905 -3.113 0.001850 \*\*

z.veg\_h\_mean:populationRemmene -0.492667 0.205125 -2.402 0.016315 \*

z.veg\_h\_mean:populationTånga Hed -0.375679 0.197066 -1.906 0.056604 .

Log(theta) 0.838236 0.141309 5.932 2.99e-09 \*\*\*

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.77174 0.19336 3.991 6.57e-05 \*\*\*

z.shoot\_h -0.40765 0.27710 -1.471 0.141250

z.veg\_h\_mean 0.19516 0.21987 0.888 0.374746

z.most\_adv -0.85002 0.25189 -3.375 0.000739 \*\*\*

z.n\_fl\_corrected -0.56217 0.35538 -1.582 0.113675

z.n\_redants 0.01267 0.17439 0.073 0.942095

z.dist\_closest\_redants -0.26592 0.25870 -1.028 0.303991

z.avg\_d\_min\_ja -0.93188 0.22196 -4.199 2.69e-05 \*\*\*

scale(prop\_pred\_num) 0.68794 0.23034 2.987 0.002821 \*\*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Theta = 2.3123

Number of iterations in BFGS optimization: 41

Log-likelihood: -814.1 on 25 Df

3) Relative importance of plant traits vs. context for explaining the variation in predispersal seed predation and in plant fitness

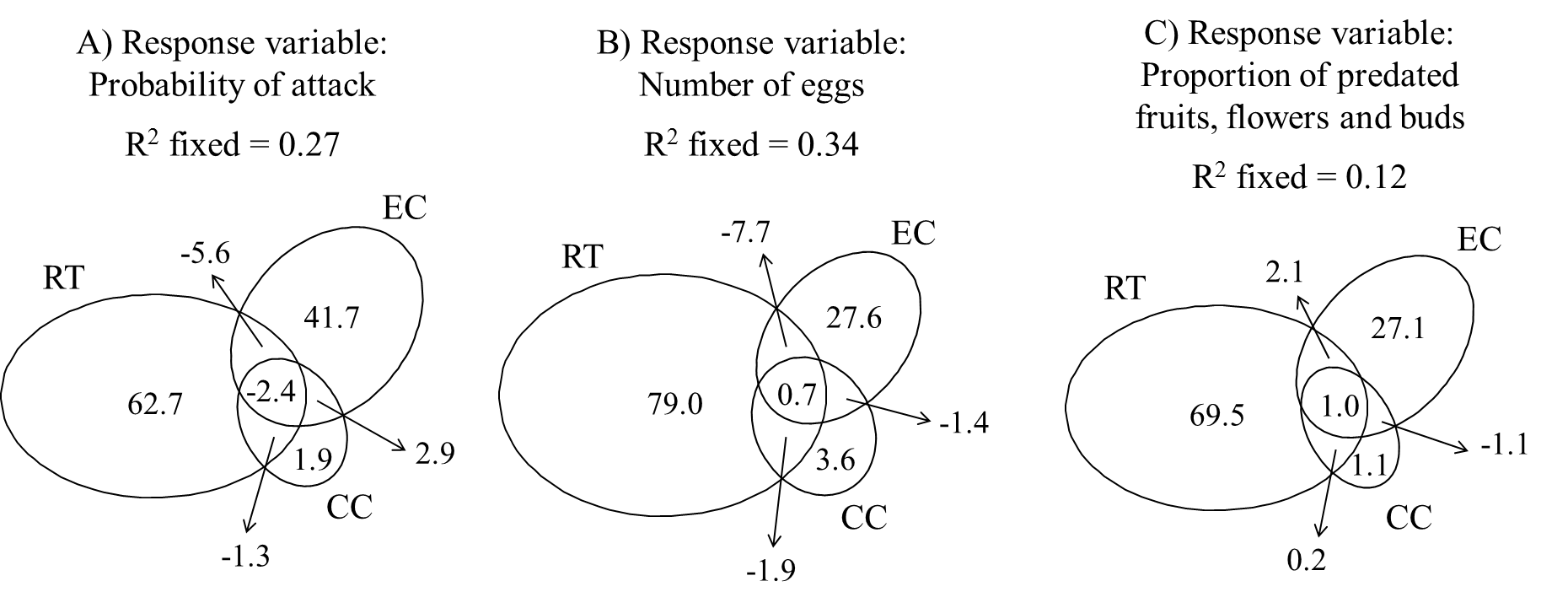
Variation partitioning analyses using GLMMs with population always as a random effect. Values shown inside the ellipses in the figures below are percentages of the total variation explained by fixed factors (R2 fixed of the model including all the variables). The calculations are made so that the percentages sum to 100%.

Response = Predispersal seed predation - 3 variable groups:

Traits: z.shoot\_h + z.most\_adv + z.n\_fl\_corrected

Environmental context: z.veg\_h\_mean + z.avg\_d\_min\_ja

Community context: z.n\_redants + z.dist\_closest\_redants



Response = Plant fitness - 3 variable groups:

Traits: z.shoot\_h + z.most\_adv + z.n\_fl\_corrected

Context: z.veg\_h\_mean + z.avg\_d\_min\_ja + z.n\_redants + z.dist\_closest\_redants (environmental + community context merged together)

Interaction: attack OR number of eggs OR prop\_predated

|  |
| --- |
|  |
|  |

For seeds: Zero-inflated model with random factors (population) is possible, but cannot get a r square (needed for the variation partitioning)

* Use 4 groups of variables? traits, context, interaction, population (hard to represent in a graph)
* Remove context variables? (as no significant effect in the model) – or remove population? (Which probably takes most of the variation)
* Use glmer with Poisson distribution? (although it fits the data quite badly)