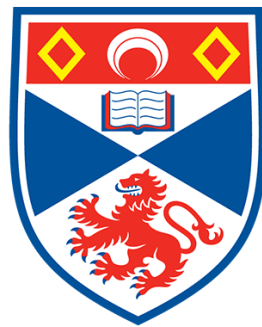# Where to See Poecile: Understanding Swiss Willow Tit Occupancy

Misha Tseitlin

25 March 2024

Project 3: Occupancy Modelling

University of
St Andrews

School of Mathematics and Statistics

Executive Summary

Switzerland is home to many willow tits (*Poecile montanus*) that have avoided population declines affecting Eurasian conspecifics. Using data from a well-structured, long-term monitoring programme, we look at 2014 willow tit occurrence and detectability across Switzerland using a single-season, single-species occupancy model. Resulting analysis confirms complex relationships between occupancy, forest cover, and elevation while hinting at unmodelled subspecies distributions. Though data limitations suggest imperfect fit and potential bias, we find that *P. montanus* generally prefers 50-70% forested areas at mid-to-high elevations, but trends differ depending on specific forest-elevation interactions. Though further accounting for land cover and climate impacts would improve our confidence, current results suggest avoiding overforestation (over 75% forest cover) in high-elevation areas. Furthermore, climate change presents a key opportunity to afforest high-elevation areas, albeit slowly, that are preferred by *P. montanus*. Of course, managers should perform these in tandem with conventional strategies like deadwood preservation to best conserve Swiss willow tits going forward.[1]

Introduction

Willow tits are a well-studied resident Eurasian breeding bird undergoing population declines in areas like Britain and Finland.[2,3] Divided into several subspecies, Swiss alpine (*montanus*) and willow tits (*rhenanus* and *salicarius*) have experienced fewer pressures and better maintained their population. Alpine tits have proven especially resilient compared against more vulnerable willow tits, possibly due to competition, changing vegetation onset, and rising temperatures.[4,5] Some environmental drivers are particularly clear: whether via species name *montanus* or French common name (mésange boréale), these tits depend on mountainous, forested habitats. Averse to competition, willow tits show strong density-dependence and preference for forest edge habitats and thus respond strongly to land use changes.[6] Using occupancy modelling, we unpack specific drivers of willow tit occurrence and detectability, provide habitat management recommendations, and estimate occupancy

Methods

The Swiss programme MHB (Monitoring Häufige Brutvögel) annually surveys 267 squares nationwide to understand bird populations: we use a pre-processed subset of 237 quadrants with detected willow tits across three survey occasions (two for high-altitude quadrants) and various possible factors including elevation, forest cover, survey duration, survey route length, and survey day.[7] Data quality may be imperfect—MHB documentation listed surveys as running from mid-April to mid-July, but our "day" measure allegedly started at the start of the year which suggests surveying outside the breeding season from January to April.[4] (Table 1) For analysis, we z-scored elevation, converted forest cover to a proportion, and assumed that survey day measures the date from 1 April rather than 1 January. As we lacked spatial quadrant locations, we forgo initial exploration of detected willow tit distribution and skip directly to occupancy.

Hierarchical occupancy modelling provided the best method of separating out tit detectability p from occupancy ψ; we needed to determine which of our observations stemmed from observer patterns versus the true underlying state process. The resulting two-tier single-season, single-species model looked across i quadrants and j survey occasions to estimate p and ψ using a

Table 1: Data Summary Statistics Split by First Occasion Detection

Variable	Overall, N = 237	Undetected, N = 170	Detected, N = 67
Occasion 2 Detected, # (%)	61 (26%)	9 (5.4%)	52 (78%)
Occasion 3 Detected, # (%)	54 (28%)	7 (5.2%)	47 (80%)
Occasion 1 Duration (min)			
Mean (SD)	229 (62)	214 (57)	266 (58)
[Min, Max]	[95, 390]	[95, 390]	[120, 390]
Occasion 2 Duration (min)			
Mean (SD)	232 (63)	217 (59)	270 (57)
[Min, Max]	[90, 391]	[90, 391]	[120, 375]
Occasion 3 Duration (min)			
Mean (SD)	232 (66)	217 (64)	265 (56)
[Min, Max]	[85, 406]	[85, 406]	[110, 360]
Length (km)			
Mean (SD)	5.10 (1.35)	5.15 (1.46)	4.99 (1.04)
[Min, Max]	[1.20, 9.40]	[1.20, 9.40]	[2.90, 8.50]
Day of Occasion 1			
Mean (SD)	38 (21)	35 (21)	45 (19)
[Min, Max]	[13, 91]	[13, 91]	[13, 87]
Day of Occasion 2			
Mean (SD)	57 (19)	55 (19)	63 (17)
[Min, Max]	[29, 102]	[29, 102]	[37, 97]
Day of Occasion 3			
Mean (SD)	69 (13)	66 (11)	75 (14)
[Min, Max]	[42, 107]	[42, 101]	[47, 107]
Forest Cover (%)			
Mean (SD)	35 (28)	30 (28)	47 (23)
[Min, Max]	[0, 98]	[0, 98]	[2, 95]
Elevation (m)			
Mean (SD)	1,183 (646)	1,047 (665)	1,526 (442)
[Min, Max]	[250, 2,750]	[250, 2,750]	[380, 2,310]

Table 2: Fitted Model Comparisons

Detection	Occupancy	AIC
p(day + dur + forest + forest*day + elev)	psi(elev + elev^2*(forest + forest^2))	382.4294
p(day + dur + forest + forest*day)	psi(elev + elev^2*(forest + forest^2))	391.1644
p(day + dur + forest + forest^2)	psi(elev + elev^2 + forest + forest^2)	392.1461
p(day + dur + forest + forest*day)	psi(elev)	392.6263
p(day + dur + forest + forest*day)	psi((elev + elev^2)*(forest + forest^2))	394.7457
p(day + dur + forest)	psi(elev + elev^2 + forest + forest^2)	400.9895
p(day + dur + forest)	psi(elev + forest)	405.8298
p(.)	psi(.)	528.9870

Note. Models include survey day, survey duration, forest cover, and elevation as well as their squared and interaction terms. Interaction terms imply including base terms (e.g., elev*forest includes elev and forest).

logistic relationship $ln(\frac{x}{1-x})$ for probabilities:

$$logit(\psi_i) = \beta_0 + \beta_1 Elevation_i + \beta_2 Elevation_i^2 + \beta_3 Forest_i + \beta_4 Forest_i^2$$
$$+ \beta_5 Forest_i Elevation_i^2 + \beta_6 Forest_i^2 Elevation_i^2$$

$$logit(p_{ij}) = \alpha_0 + \alpha_1 Day_{ij} + \alpha_2 Duration_{ij} + \alpha_3 Forest_{ij} + \alpha_4 Forest_{ij} Day_{ij}$$

Detection and state functions, based on only four covariates, demonstrated the complexity of fitting highly non-linear relationships using this linear (GLM) framework fitted with `unmarked` in `R`.[8,9] To account for clear non-linearities in forest cover and elevation, we manually and automatically compared all models containing potentially relevant covariates.[10,11] Overall, adding non-linearity substantially improved model fit measured by AIC. (Table 2) Finally, we tackled model suitability using Pearson's chi-squared via bootstrap estimation: MacKenzie-Bailey goodness-of-fit tests measured the chance of seeing our data given the model via a p-value and resulting overdispersion $\hat{c}$.[12] To correct for imperfect fit, we inflated errors by $\hat{c}$.[13]
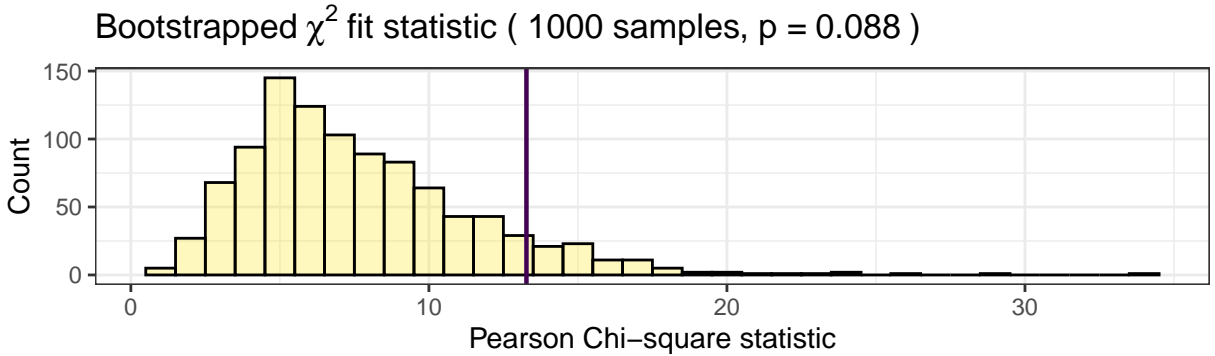

Figure 1: Goodness-of-fit suggests 'good' yet somewhat atypical model fit at the 5% level.

Results

Overall, our model is passable but suggests violated assumptions. On one hand, we understand covariates like forest*day interactions for detection (i.e., foliage density affects plumage camouflage) and occupancy impacts from squared relationships with elevation (i.e., optimal mountain habitat below the tree line) and forests (i.e., higher competition and less deadwood

in aggressively-forested areas). The joint relationship between both forest and elevation further approximates miscellaneous ecosystem suitability like climate and diet.[14] Nonetheless, we avoid overfitting despite AIC suggesting elevation-dependent detection. Elevation indeed affects cloud cover, heat, and humidity and therefore detection (by proxy) but imperfectly captures these effects.[15,16] Instead, identifiability issues inhibit parameter-specific inference; more importantly, overfit empirical performance implies unmodelled detection heterogeneity and occupancy underestimates.[13,17] Thus, fit suggests omitted explanatory covariates (e.g., climate, subspecies) violate independence across sites and occasions despite some promising goodness-of-fit results. (Figure 1) Nonetheless, our model balances predictive and inferential goals: imperfectly matching the data may better generalise beyond anomalous 2014 heat and vegetation.
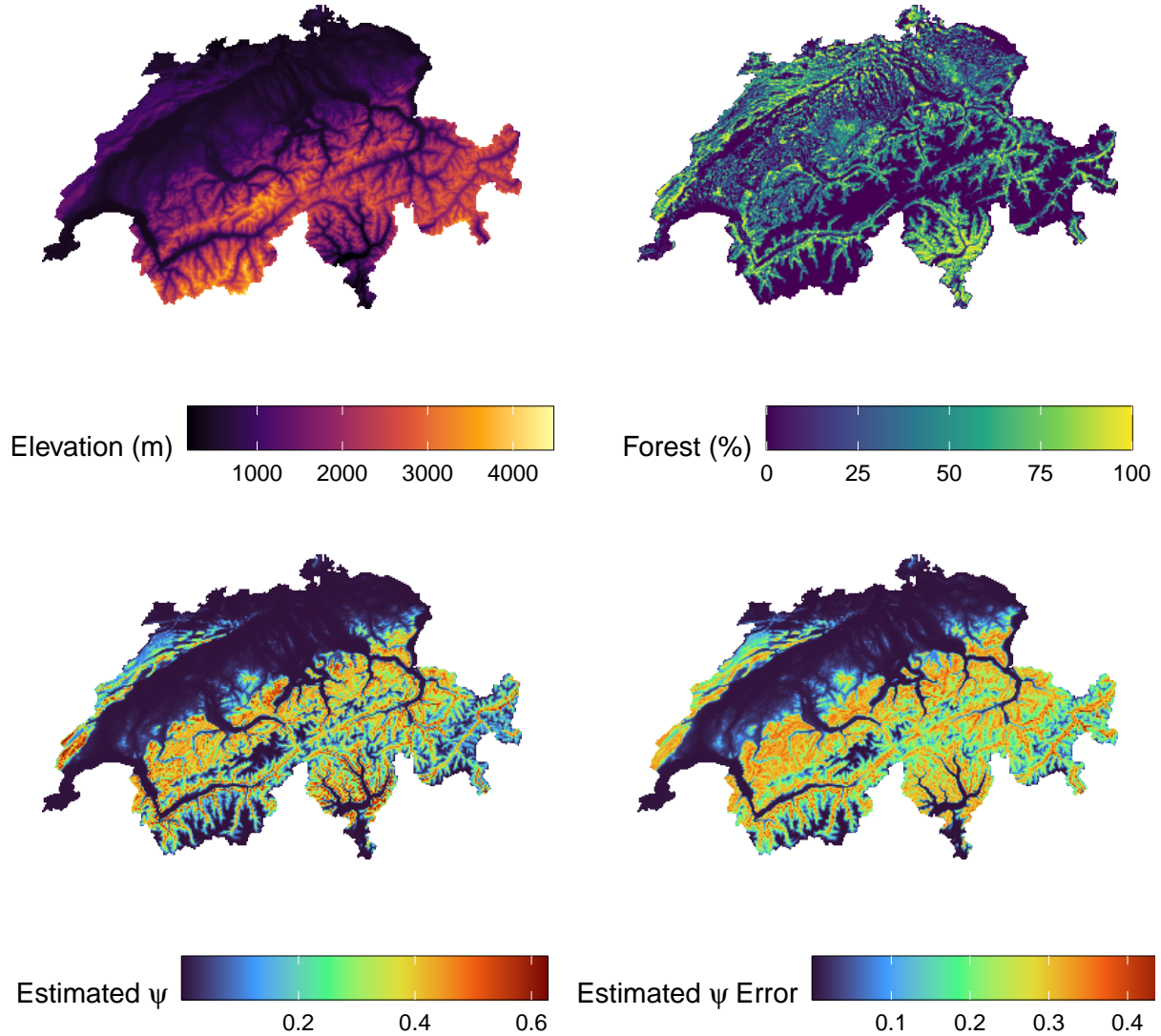

Figure 2: Spatial trends of elevation, forest cover, and estimated occupancy across Switzerland.

Given non-linear parameter estimates, we first examine spatial occupancy estimates. First, estimates cannot differentiate between the southern Swiss Alps's alpine tit and the willow tit in northwestern Jura and central pre-Alps and may drive complex parameter nonlinearities—intermediate elevation with high forest in the former, but intermediate vegetation with high elevation in the latter. (Figure 2) Overall, we struggle to conclude anything beyond tit avoidance of low-lying river valleys and the Central Plateau; estimated occupancy peaks above 50% only around Jura Vadois in the west, surrounding Rhone and Ticino river valleys in the south, and upslope Lake Lucerne's surrounding Pre-Alps. (Figure 3)
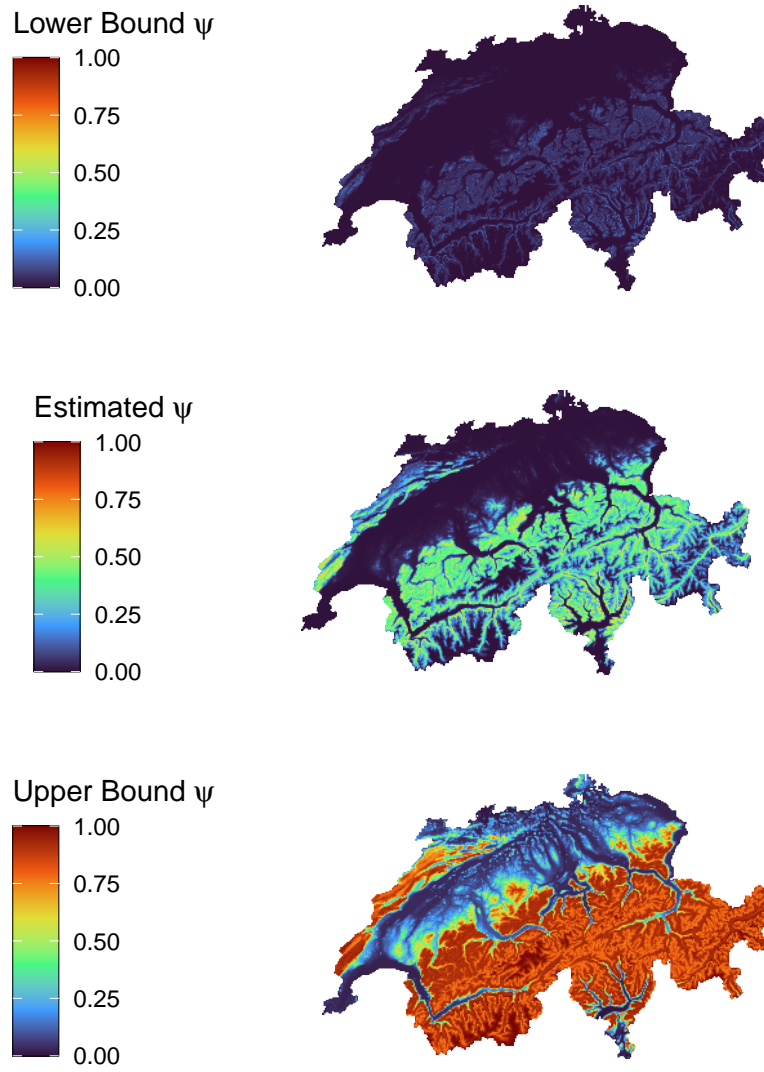
Figure 3: Mean, upper, and lower bound predicted occupancy demonstrating extreme uncertainty and few high-confidence areas. Colour axes are rescaled to facilitate clear absolute comparisons.

Table 3: Four Quadrant-Specific Willow Tit Occupancy (Psi) Predictions

Quadrant	Pred Psi	Psi Error	Psi Lower	Psi Upper	Elevation (m)	Forest (%)
25	0.011	0.015	0.001	0.155	620	3
62	0.012	0.012	0.002	0.078	370	14
150	0.790	0.131	0.443	0.947	1660	86
203	0.693	0.210	0.246	0.940	1980	6

Note. Only quadrant 203 detected a willow tit, while other quadrants had no detections.

Looking at (spatially ambiguous) quadrant-specific willow tit occupancy, quadrants 25 and 62 have extremely low occupancy due to few trees and low elevation. In contrast, quadrants 150 and 203 show more uncertainty at extreme values of forest cover and elevation; however, best estimates suggest that willow tits more likely occupy than not. (Table 3)

Detection partial effects elucidate data limitations and future collection strategies: observers detect more tits later in forested areas due to contrast between brown-grey plumage and slowly emerging green foliage, yet in theory, foliage-obscured visibility may act contrarily too. (Figure 4) Of course, longer surveys detect more, and time matters more than omitted survey length. (Figure 5) For occupancy, higher elevations single-handedly increase occupancy and further determine forestation affects. At low and high elevations, willow tits prefer 50% forest cover but stomach more substantial 60-70% forest cover along intermediate elevation. (Figure 6) Of course, both elevation and forest cover demonstrate huge uncertainty at hint at model weaknesses: in spite of results, no trees reside above 2500 metres in Switzerland, and some local tree lines start at 1300 m.[18] Conversely, assisted upslope migration via deliberate afforestation can create ideal, non-competitive environments for willow tits given climate change. Though natural upslope migration stops at 100 m past the Swiss tree line, deliberately introducing hardy trees—high-elevation pines like *Pinus cembra*—would enable deciduous tree recruitment at higher altitudes.[19]

On net, covariates poorly capture spatio-temporal variation across quadrants and occasions but provide some insights into elevation and forest cover dependencies in willow tit occupancy. Though assumption violations threaten substantial inference, management regimes may (1) avoid overforesting suitable habitats, and (2) afforest high-elevation areas to support tree line increases and expand preferred willow tit habitat. Of course, future analyses would ideally test the impact of land cover and climate on occupancy to validate such anthropogenic interventions.[4]
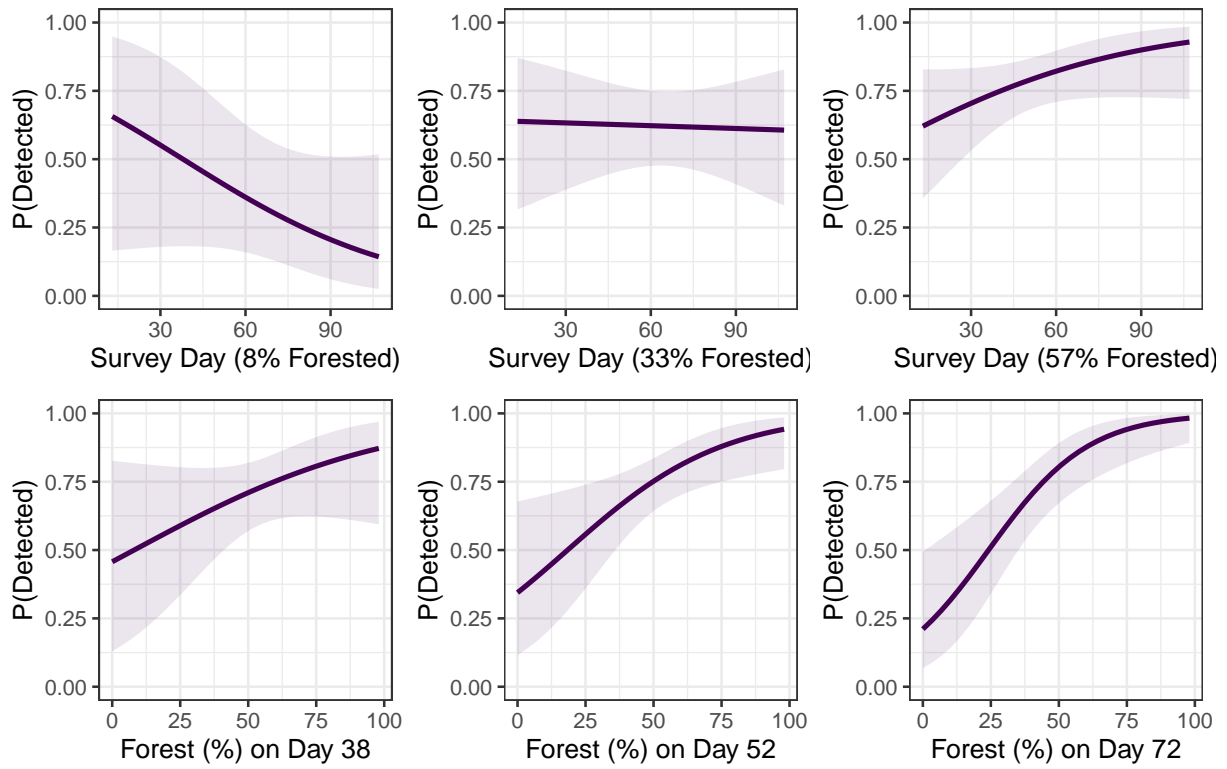
Figure 4: Survey day and forest effects on detection under 25th, median, and 75th percentile values of non-axis variables. Detection may increase with forest cover due to plumage—willow tits better camoflauge under greys and browns than greens. On early survey days with less foliage in forested areas, detection is harder, while possible weather or climate effects like snow melts exposing rock surfaces may drive lower detection in the absence of forest ecosystem greenery.

Figure 5: Longer surveys increase detection more so than surveying longer routes or doing so more intensely.

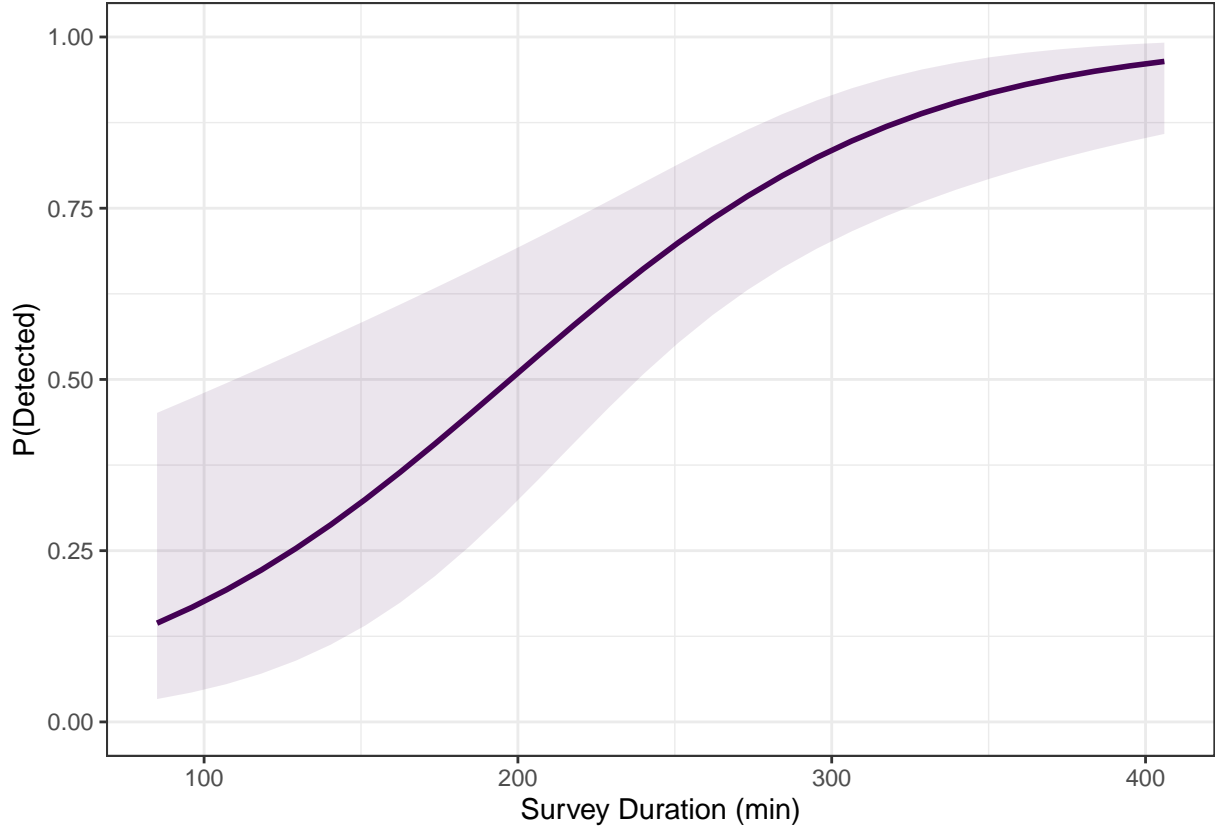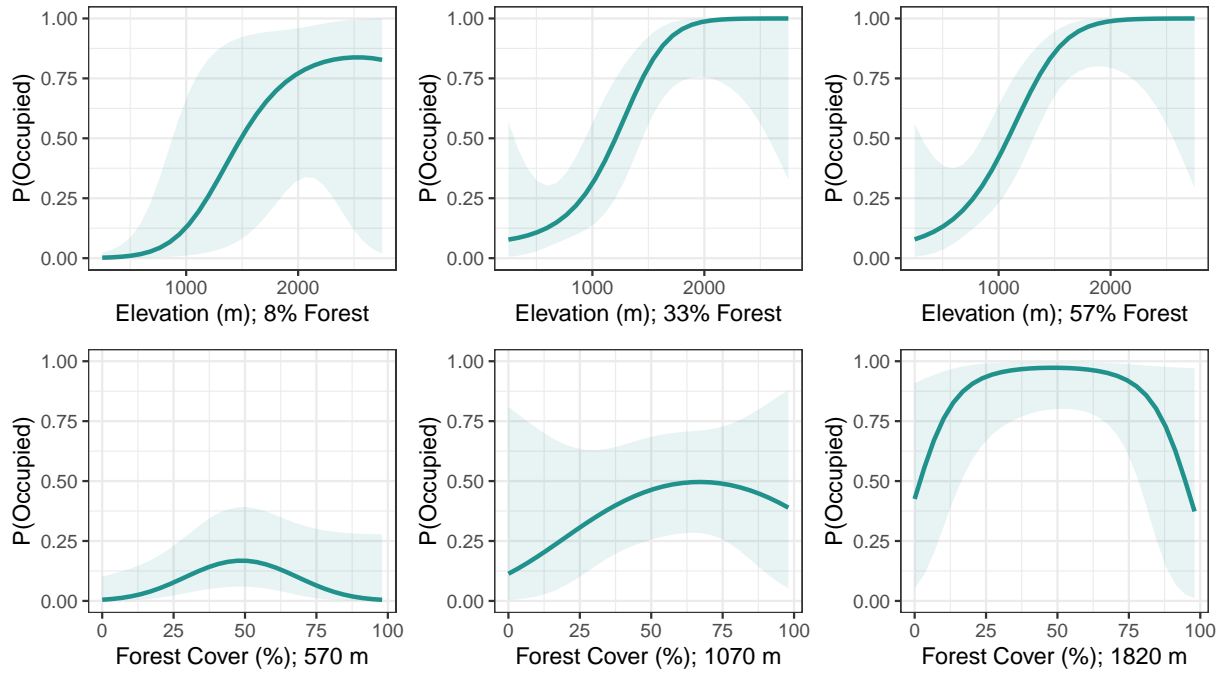
Figure 6: Elevation and forest effects on latent occupancy under 25th, median, and 75th percentile values of the non-axis variable. Elevation is essential to occupancy but highly uncertain at extreme values, while forest cover's effects are clearer but with elevation-dependent magnitudes.

Code Appendix

```r
library(statsecol)
library(unmarked)
library(tidyverse)
library(MuMIn)
library(AICcmodavg)
library(viridisLite)
library(latex2exp)
# read in data
data(willow)
# prepare the data how I need it
willowNum <- willow %>% mutate(forestsq = forest^2,
                               iLength = 1/length) %>%
  mutate_all(as.numeric) %>%
  rownames_to_column("id")

willowSum <- willowNum %>% mutate(forestP = forest*100,
                                  elevR = 1182.574 + elev*646.333,
                                  y.1 = as.factor(y.1),
                                  y.2 = as.factor(y.2),
                                  y.3 = as.factor(y.3)) %>%
  select(-c("id","elev","elevsq","forest","forestsq","iLength"))

# brief data visualisation
hist(willowNum$forest)
hist(willowNum$elev)
hist(willowNum$length)
# no clear relationship here, except no forest at very high-elevation areas
ggplot(willowNum, aes(x = forest, y = elev)) + geom_point()
# no occurrence at lower elevations, higher occurrence at higher elevations
# no real shifts between time periods
ggplot(willowNum, aes(x = elev, fill = y.1)) +
  geom_histogram() +
  facet_wrap(~y.1) +
  theme(legend.position = "")
ggplot(willowNum, aes(x = elev, fill = y.2)) +
  geom_histogram() +
  facet_wrap(~y.2) +
  theme(legend.position = "")
ggplot(willowNum, aes(x = elev, fill = y.3)) +
  geom_histogram() +
  facet_wrap(~y.3) +
  theme(legend.position = "")
# complex forest relationship
# no occurrence at predominantly low forest cover
# an inverse relationship across forest cover types
# no shifts between time periods again
ggplot(willowNum, aes(x = forest, fill = y.1)) +
  geom_histogram() +
  facet_wrap(~y.1) +
```

```r
  theme(legend.position = "")
ggplot(willowNum, aes(x = forest, fill = y.2)) +
  geom_histogram() +
  facet_wrap(~y.2) +
  theme(legend.position = "")
ggplot(willowNum, aes(x = forest, fill = y.3)) +
  geom_histogram() +
  facet_wrap(~y.3) +
  theme(legend.position = "")




willowUnm <- unmarkedFrameOccu(
  y = willowNum[,c("y.1","y.2","y.3")],
  # we are interested in breeding bird occupancy for the WHOLE breeding season
  # days (occasion-specific) are not good site covariates in this case
  siteCovs = data.frame(elev = willowNum$elev,
                        elev2 = willowNum$elevsq,
                        forest = willowNum$forest,
                        forest2 = willowNum$forestsq,
                        iLength = willowNum$iLength),
  obsCovs = list(day = willowNum[,c("day1","day2","day3")],
                 dur = willowNum[,c("dur1","dur2","dur3")],
                 intensity = willowNum[,c("intensity1",
                                          "intensity2",
                                          "intensity3")],
                 length = willowNum[,c("length","length","length")],
                 iLength = willowNum[,c("iLength","iLength","iLength")],
                 forest = willowNum[,c("forest","forest","forest")],
                 forest2 = willowNum[,c("forestsq","forestsq","forestsq")],
                 elev = willowNum[,c("elev","elev","elev")],
                 elev2 = willowNum[,c("elevsq","elevsq","elevsq")])
)
summary(willowUnm)

# some more plotting
hist(willowUnm@obsCovs$day)
hist(willowUnm@obsCovs$dur)
hist(willowUnm@obsCovs$intensity)


# null model
m0 <- occu(~1 ~1, data = willowUnm)

# full model
# intensity:length interaction is just dur and thus not included
mfull <- occu(formula = ~day + dur + intensity + length + day*dur +
                dur*intensity + day*length + day*intensity +
                dur*length  # p formula
              ~elev + elev2 + forest + forest2 + elev*forest +
                elev2*forest2 + elev*forest2 + elev2*forest, #psi formula
```

```r
                  data = willowUnm) #the data object

summary(mfull)

# all three agree on a few things
# elev2 and elev:forest are mutually exclusive
# p(day) is not worth including
# all p interaction terms are useless
mDredgeB <- dredge(mfull, rank = "BIC")
mDredgeA <- dredge(mfull, rank = "AIC")
mDredgeAc <- dredge(mfull, rank = "AICc")


mBIC <- occu(formula = ~dur # p formula
             ~elev + forest + forest^2 + elev*forest, #psi formula
             data = willowUnm) #the data object
summary(mBIC)

# we missed a few variables, mainly forests which could affect visibility
# (even though it also influences true occupancy)
mfullAct <- occu(formula = ~day + dur + intensity + length + day*dur +
                    dur*intensity + day*length + day*intensity + dur*length +
                    forest + forest*dur + forest*day + forest*intensity +
                    forest*length # p formula
                 ~elev + elev2 + forest + forest2 + elev*forest + elev2*forest2 +
                   elev*forest2 + elev2*forest, #psi formula
                 data = willowUnm) #the data object

summary(mfullAct)

# all three agree on a few things
# elev2 and elev:forest are mutually exclusive
# p(day) is not worth including
# all p interaction terms are useless
mDredgeB2 <- dredge(mfullAct, rank = "BIC")
mDredgeA2 <- dredge(mfullAct, rank = "AIC")
mDredgeAc2 <- dredge(mfullAct, rank = "AICc")

# create some representative models to display
mAlt <- occu(formula = ~day + dur + forest  # p formula
             ~elev + forest, #psi formula
             data = willowUnm) #the data object


mAlt1 <- occu(formula = ~day + dur + forest # p formula
              ~elev + elev2 + forest + forest2, #psi formula
              data = willowUnm) #the data object


mAlt2 <- occu(formula = ~day + dur + forest + forest2 # p formula
              ~elev + elev2 + forest + forest2, #psi formula
              data = willowUnm) #the data object


mOptm_Alt <- occu(formula = ~day + dur + forest + forest*day # p formula
```

11

```r
                     ~elev, #psi formula
                     data = willowUnm) #the data object


# recording visibility/leafing may be a good way to increase separability
# maybe avoid forest in both models?
mOptm <- occu(formula = ~day + dur + forest + forest*day # p formula
              #psi formula
              ~elev + elev2 + forest + forest2 + elev2*forest + elev2*forest2,
              data = willowUnm) #the data object


mAlt3 <- occu(formula = ~day + dur + forest + forest*day # p formula
              ~elev + elev2 + forest + forest2 + elev*forest +
                elev*forest2 + elev2*forest + elev2*forest2 , #psi formula
              data = willowUnm) #the data object


# by far the best model, but elevation in the detection function is too much
mOverpred <- occu(formula = ~day + dur + forest + forest*day + elev # p formula
              ~elev + elev2 + forest + forest2 +
                elev2*forest + elev2*forest2 , #psi formula
              data = willowUnm) #the data object


# combine some representative models for displaying
fl <- fitList(
  "p(.)                                     psi(.)"
  "p(day + dur + forest)                    psi(elev + forest)"
  "p(day + dur + forest)                    psi(elev + elev^2 + forest + forest^2)"
  "p(day + dur + forest + forest^2)         psi(elev + elev^2 + forest + forest^2)"
  "p(day + dur + forest + forest*day)       psi(elev)"
  "p(day + dur + forest + forest*day)       psi(elev + elev^2*(forest + forest^2))"
  "p(day + dur + forest + forest*day)       psi((elev + elev^2)*(forest + forest^2))"
  "p(day + dur + forest + forest*day + elev)  psi((elev + elev^2)*(forest + forest^2))"


# model output table to format
ms <- modSel(fl)


# full model summary
summary(mOptm)
# state model
mOptm@estimates@estimates$state
#detection model
mOptm@estimates@estimates$det


# test for VIF?
# so much strutural collinearity that this probably doesn't matter
vif(mOptm, type = "state")
vif(mOptm, type = "det")


# GOF for best model....it's barely passable
# code below is parallelised, be careful all ye who lack 10 free cores
gof.boot <- mb.gof.test(mOptm, nsim = 1000, ncores = 10)
# save this and re-use output out of pity for my computer
```

```r
write_rds(gof.boot, file = "gofBootstrap.rds")
# p-values generally vary between 0.4 and 0.9, but negligible chat difference
# 10000 cores confirms a p-value around 0.7 but the plot is too ugly
# gof.boot <- mb.gof.test(mOptm, nsim = 10000, ncores = 10)



# repeat for the overfit model
# fit is so temptingly good...but it just doesn't make sense
gof.boot.test <- mb.gof.test(mOverpred, nsim = 10000, ncores = 10)
write_rds(gof.boot.test, file = "gofBootstrapOverfit.rds")

# read in the saved for analysis
gof.boot <- read_rds("gofBootstrap.rds")
# even so, our model is very much closer to the tail of the chi^2 distribution
# p-value may be deceiptive, the plot is a good visual
ggplot() +
  geom_histogram(data = data.frame(t.star = gof.boot$t.star),
                 aes(x=t.star),
                 color="black",
                 fill="#fde725",
                 alpha = 0.3,
                 binwidth = 1) +
  geom_vline(aes(xintercept = gof.boot$chi.square),
             linewidth = 0.8,
             color = "#440154") +
  xlab("Pearson Chi-square statistic") +
  ylab("Count") +
  theme_bw() +
  ggtitle(
    bquote("Bootstrapped"~chi^2~"fit statistic (1000 samples, p ="~.(gof.boot$p.valu)~")")
    )

#start spatial plotting
data(Switzerland) # import Swiss data
gelev <- ggplot(data = Switzerland, aes(x=x, y=y,fill=elevation)) +
  geom_raster() +
  scale_fill_viridis_c(direction = 1,
                       option = "B") +
  theme_bw() +
  theme(axis.text = element_blank(),
        axis.line = element_blank(),
        axis.ticks = element_blank(),
        panel.grid = element_blank(),
        panel.border = element_blank(),
        legend.position = "bottom") +
  labs(x = "",
       y = "",
       fill = "Elevation (m)") +
  guides(fill = guide_colorbar(# draw border around the legend
                               frame.colour = "black",
```

```r
                                       barwidth = 10)) +
  coord_fixed() # don't play around w/ dimensions
gfor <- ggplot(data = Switzerland, aes(x=x, y=y,fill=forest)) +
  geom_raster() +
  scale_fill_viridis_c(direction = 1,
                       option = "D") +
  theme_bw() +
  theme(axis.text = element_blank(),
        axis.line = element_blank(),
        axis.ticks = element_blank(),
        panel.grid = element_blank(),
        panel.border = element_blank(),
        legend.position="bottom") +
  labs(x = "",
       y = "",
       fill = "Forest (%)")  +
  guides(fill = guide_colorbar(# draw border around the legend
    frame.colour = "black",
    barwidth = 10)) +
  coord_fixed()
                       # convert original m to z-score
for_pred <- data.frame(elev = (Switzerland$elevation - 1182.574)/646.333,
                       # convert original m to z-score
                       elev2 = ((Switzerland$elevation - 1182.574)/646.333)^2,
                       #want prop not %
                       forest = Switzerland$forest/100,
                       #want prop not %
                       forest2 = Switzerland$forest/100,
                       X = Switzerland$x,        #keep the coordinates
                       Y = Switzerland$y)        #keep the coordinates
cowplot::plot_grid(gelev,gfor,nrow=2)

willowPredSDM <- modavgPred(list(mOptm), # top model
                            newdata = for_pred, #spatially indexed data frame
                            parm.type = "psi",  #predict from state model
                            c.hat = gof.boot$c.hat.est) #to inflate SEs
# save to speed up compiling
write_rds(willowPredSDM, file = "willowPred.rds")
# read in the saved for analysis
willowPredSDM <- read_rds("willowPred.rds")

#add data to predictions manually
willow_sdm <- for_pred %>% mutate(Predicted = willowPredSDM$mod.avg.pred,
                                  SE = willowPredSDM$uncond.se,
                                  lower = willowPredSDM$lower.CL,
                                  upper = willowPredSDM$upper.CL)

gpredM_1 <- ggplot(data = willow_sdm, aes(x=X, y=Y,fill=Predicted)) +
  geom_raster() +
  scale_fill_viridis_c(direction = 1,
                       option = "H") +
```

```r
    # add actual observations if we have x,y data
    # geom_point(data = willowNum, aes(x=X, y=Y)) +
    theme_bw() +
    theme(axis.text = element_blank(),
          axis.line = element_blank(),
          axis.ticks = element_blank(),
          panel.grid = element_blank(),
          panel.border = element_blank(),
          legend.position="bottom") +
    labs(x = "",
         y = "",
         fill = TeX(r'(Estimated $\psi$)'))  +
    guides(fill = guide_colorbar(# draw border around the legend
      frame.colour = "black",
      barwidth = 10)) +
    coord_fixed()

gpredE <- ggplot(data = willow_sdm, aes(x=X, y=Y,fill=SE)) +
    geom_raster() +
    scale_fill_viridis_c(direction = 1,
                         option = "H") +
    theme_bw() +
    theme(axis.text = element_blank(),
          axis.line = element_blank(),
          axis.ticks = element_blank(),
          panel.grid = element_blank(),
          panel.border = element_blank(),
          legend.position="bottom") +
    labs(x = "",
         y = "",
         fill = TeX(r'(Estimated $\psi$ Error)'))  +
    guides(fill = guide_colorbar(# draw border around the legend
      frame.colour = "black",
      barwidth = 10)) +
    coord_fixed()

cowplot::plot_grid(gelev,gfor,gpredM_1,gpredE,nrow=2)

gpredL <- ggplot(data = willow_sdm, aes(x=X, y=Y,fill=lower)) +
    geom_raster() +
    scale_fill_viridis_c(direction = 1,
                         option = "H",
                         limits= c(0,1)) +
    theme_bw() +
    theme(axis.text = element_blank(),
          axis.line = element_blank(),
          axis.ticks = element_blank(),
          panel.grid = element_blank(),
          panel.border = element_blank(),
          legend.position="left") +
    labs(x = "",
```

```r
      y = "",
      fill = TeX(r'(Lower Bound $\psi$)')) +
  guides(fill = guide_colorbar(# draw border around the legend
    frame.colour = "black")) +
  coord_fixed()


gpredM_2 <- ggplot(data = willow_sdm, aes(x=X, y=Y,fill=Predicted)) +
  geom_raster() +
  scale_fill_viridis_c(direction = 1,
                       option = "H",
                       limits= c(0,1)) +
  # add actual observations if we have x,y data
  # geom_point(data = willowNum, aes(x=X, y=Y)) +
  theme_bw() +
  theme(axis.text = element_blank(),
        axis.line = element_blank(),
        axis.ticks = element_blank(),
        panel.grid = element_blank(),
        panel.border = element_blank(),
        legend.position="left") +
  labs(x = "",
       y = "",
       fill = TeX(r'(Estimated $\psi$)'))  +
  guides(fill = guide_colorbar(# draw border around the legend
    frame.colour = "black")) +
  coord_fixed()


gpredH <- ggplot(data = willow_sdm, aes(x=X, y=Y,fill=upper)) +
  geom_raster() +
  scale_fill_viridis_c(direction = 1,
                       option = "H",
                       limits= c(0,1)) +
  theme_bw() +
  theme(axis.text = element_blank(),
        axis.line = element_blank(),
        axis.ticks = element_blank(),
        panel.grid = element_blank(),
        panel.border = element_blank(),
        legend.position="left") +
  labs(x = "",
       y = "",
       fill = TeX(r'(Upper Bound $\psi$)'))  +
  guides(fill = guide_colorbar(# draw border around the legend
    frame.colour = "black")) +
  coord_fixed()


cowplot::plot_grid(gpredL, gpredM_2, gpredH,nrow=3)



# plot marginal effects
#-----------------------------------------------------------------------------#
```

```r
#psi ~ elev | quantiles(forest)
pred_psi_eleL <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        max(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        length = 30),
                            forest = quantile(probs = 0.25,
                                              willowUnm@siteCovs$forest,
                                              na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiEleL <- modavgPred(list(mOptm),
                          newdata = pred_psi_eleL,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleL <- pred_psi_eleL %>% mutate(Predicted = predPsiEleL$mod.avg.pred,
                                          SE = predPsiEleL$uncond.se,
                                          lower = predPsiEleL$lower.CL,
                                          upper = predPsiEleL$upper.CL,
                                          elevR = 1182.574 + elev*646.333)
ggpsieleL <- ggplot(data = pred_psi_eleL, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") +
  xlab("Elevation (m); 8% Forest") +
  ylim(0,1) +
  theme_bw()
# repeat for median
pred_psi_eleM <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        max(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        length = 30),
                            forest = median(willowUnm@siteCovs$forest,
                                            na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiEleM <- modavgPred(list(mOptm),
                          newdata = pred_psi_eleM,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleM <- pred_psi_eleM %>% mutate(Predicted = predPsiEleM$mod.avg.pred,
                                          SE = predPsiEleM$uncond.se,
                                          lower = predPsiEleM$lower.CL,
                                          upper = predPsiEleM$upper.CL,
                                          elevR = 1182.574 + elev*646.333)
ggpsieleM <- ggplot(data = pred_psi_eleM, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") +
  xlab("Elevation (m); 33% Forest") +
```

```r
  ylim(0,1) +
  theme_bw()
# repeat for 75th percentile
pred_psi_eleH <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        max(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                        length = 30),
                             forest = quantile(probs = 0.75,
                                               willowUnm@siteCovs$forest,
                                               na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiEleH <- modavgPred(list(mOptm),
                          newdata = pred_psi_eleH,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleH <- pred_psi_eleH %>% mutate(Predicted = predPsiEleH$mod.avg.pred,
                                          SE = predPsiEleH$uncond.se,
                                          lower = predPsiEleH$lower.CL,
                                          upper = predPsiEleH$upper.CL,
                                          elevR = 1182.574 + elev*646.333)
ggpsieleH <- ggplot(data = pred_psi_eleH, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") +
  xlab("Elevation (m); 57% Forest") +
  ylim(0,1) +
  theme_bw()


#-----------------------------------------------------------------------------#
#psi ~ for | quantiles(elev)
pred_psi_forL <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                             na.rm=TRUE),
                                          max(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                          length = 30),
                             elev = quantile(probs = 0.25,
                                             willowUnm@siteCovs$elev,
                                             na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForL <- modavgPred(list(mOptm), newdata = pred_psi_forL,
                          parm.type = "psi", c.hat = gof.boot$c.hat.est)
pred_psi_forL <- pred_psi_forL %>% mutate(Predicted = predPsiForL$mod.avg.pred,
                                          SE = predPsiForL$uncond.se,
                                          lower = predPsiForL$lower.CL,
                                          upper = predPsiForL$upper.CL,
                                          forestP = forest*100)
ggpsiforL <- ggplot(data = pred_psi_forL, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
```

```r
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%); 570 m") + ylim(0,1) + theme_bw()

pred_psi_forM <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         max(willowUnm@siteCovs$forest,
                                             na.rm=TRUE),
                                         length = 30),
                            elev = median(willowUnm@siteCovs$elev,
                                          na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForM <- modavgPred(list(mOptm), newdata = pred_psi_forM,
                          parm.type = "psi", c.hat = gof.boot$c.hat.est)
pred_psi_forM <- pred_psi_forM %>% mutate(Predicted = predPsiForM$mod.avg.pred,
                                          SE = predPsiForM$uncond.se,
                                          lower = predPsiForM$lower.CL,
                                          upper = predPsiForM$upper.CL,
                                          forestP = forest*100)
ggpsiforM <- ggplot(data = pred_psi_forM, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%); 1070 m") +
  ylim(0,1) +
  theme_bw()

pred_psi_forH <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         max(willowUnm@siteCovs$forest,
                                             na.rm=TRUE),
                                         length = 30),
                            elev = quantile(probs = 0.75,
                                            willowUnm@siteCovs$elev,
                                            na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForH <- modavgPred(list(mOptm), newdata = pred_psi_forH,
                          parm.type = "psi", c.hat = gof.boot$c.hat.est)
pred_psi_forH <- pred_psi_forH %>% mutate(Predicted = predPsiForH$mod.avg.pred,
                                          SE = predPsiForH$uncond.se,
                                          lower = predPsiForH$lower.CL,
                                          upper = predPsiForH$upper.CL,
                                          forestP = forest*100)
ggpsiforH <- ggplot(data = pred_psi_forH, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%); 1820 m") + ylim(0,1) +
  theme_bw()

cowplot::plot_grid(ggpsieleL, ggpsieleM, ggpsieleH,
                   ggpsiforL, ggpsiforM, ggpsiforH, nrow=2)
```

```r
# now onto detection
#-----------------------------------------------------------------------#
#p ~ dur | median(day & forest)
pred_p_dur <- data.frame(dur = seq(min(willowUnm@obsCovs$dur, na.rm=TRUE),
                                   max(willowUnm@obsCovs$dur, na.rm=TRUE),
                                   length = 30),
                         day = median(willowUnm@obsCovs$day, na.rm=TRUE),
                         forest = median(willowUnm@obsCovs$forest,
                                         na.rm=TRUE))
predPDur <- modavgPred(list(mOptm), newdata = pred_p_dur, parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_dur <- pred_p_dur %>% mutate(Predicted = predPDur$mod.avg.pred,
                                    SE = predPDur$uncond.se,
                                    lower = predPDur$lower.CL,
                                    upper = predPDur$upper.CL,
                                    forestP = forest*100)
pDurPlot <- ggplot(data = pred_p_dur, aes(x = dur, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Survey Duration (min)") + ylim(0,1) + theme_bw()
#-----------------------------------------------------------------------#
#p ~ day | median(dur & forest)
pred_p_dayL <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                    max(willowUnm@obsCovs$day, na.rm=TRUE),
                                    length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          forest = quantile(probs = 0.25,
                                            willowUnm@obsCovs$forest,
                                            na.rm=TRUE))
predPDayL <- modavgPred(list(mOptm), newdata = pred_p_dayL,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_dayL <- pred_p_dayL %>% mutate(Predicted = predPDayL$mod.avg.pred,
                                      SE = predPDayL$uncond.se,
                                      lower = predPDayL$lower.CL,
                                      upper = predPDayL$upper.CL,
                                      forestP = forest*100)
pDayPlotL <- ggplot(data = pred_p_dayL, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") +
  xlab("Survey Day (8% Forested)") +
  ylim(0,1) +
  theme_bw()
#p ~ day | Q2(dur & forest)
pred_p_day <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                   max(willowUnm@obsCovs$day, na.rm=TRUE),
                                   length = 30),
                         dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
```

```r
                              forest = quantile(probs = 0.5,
                                                willowUnm@obsCovs$forest,
                                                na.rm=TRUE))
predPDay <- modavgPred(list(mOptm), newdata = pred_p_day,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_day <- pred_p_day %>% mutate(Predicted = predPDay$mod.avg.pred,
                                    SE = predPDay$uncond.se,
                                    lower = predPDay$lower.CL,
                                    upper = predPDay$upper.CL,
                                    forestP = forest*100)
pDayPlot <- ggplot(data = pred_p_day, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Survey Day (33% Forested)") + ylim(0,1) +
  theme_bw()
#p ~ day | Q4(dur & forest)
pred_p_dayH <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                    max(willowUnm@obsCovs$day, na.rm=TRUE),
                                    length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          forest = quantile(probs = 0.75,
                                            willowUnm@obsCovs$forest,
                                            na.rm=TRUE))
predPDayH <- modavgPred(list(mOptm), newdata = pred_p_dayH,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_dayH <- pred_p_dayH %>% mutate(Predicted = predPDayH$mod.avg.pred,
                                      SE = predPDayH$uncond.se,
                                      lower = predPDayH$lower.CL,
                                      upper = predPDayH$upper.CL,
                                      forestP = forest*100)
pDayPlotH <- ggplot(data = pred_p_dayH, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Survey Day (57% Forested)") + ylim(0,1) +
  theme_bw()
#----------------------------------------------------------------------------#
#p ~ for | Q2(day), median(dur)
pred_p_forL <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                       max(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                       length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          day = quantile(probs = 0.25,
                                         willowUnm@obsCovs$day,
                                         na.rm=TRUE))
predPForL <- modavgPred(list(mOptm), newdata = pred_p_forL,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
```

```r
pred_p_forL <- pred_p_forL %>% mutate(Predicted = predPForL$mod.avg.pred,
                                      SE = predPForL$uncond.se,
                                      lower = predPForL$lower.CL,
                                      upper = predPForL$upper.CL,
                                      forestP = forest*100)
pForPlotL <- ggplot(data = pred_p_forL, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 38") + ylim(0,1) + theme_bw()
#p ~ for | median(dur & day)
pred_p_for <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                      max(willowUnm@obsCovs$forest,
                                          na.rm=TRUE),
                                      length = 30),
                         dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                         day = quantile(probs = 0.5,
                                        willowUnm@obsCovs$day,
                                        na.rm=TRUE))
predPFor <- modavgPred(list(mOptm), newdata = pred_p_for,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_for <- pred_p_for %>% mutate(Predicted = predPFor$mod.avg.pred,
                                    SE = predPFor$uncond.se,
                                    lower = predPFor$lower.CL,
                                    upper = predPFor$upper.CL,
                                    forestP = forest*100)
pForPlot <- ggplot(data = pred_p_for, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 52") + ylim(0,1) + theme_bw()
#p ~ for | Q4(day), median(dur)
pred_p_forH <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                       max(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                       length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          day = quantile(probs = 0.75,
                                         willowUnm@obsCovs$day,
                                         na.rm=TRUE))
predPForH <- modavgPred(list(mOptm), newdata = pred_p_forH,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_forH <- pred_p_forH %>% mutate(Predicted = predPForH$mod.avg.pred,
                                      SE = predPForH$uncond.se,
                                      lower = predPForH$lower.CL,
                                      upper = predPForH$upper.CL,
                                      forestP = forest*100)
ggplot(data = pred_p_forH, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
```

```r
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 72") + ylim(0,1) + theme_bw()

# all together
cowplot::plot_grid(pDayPlotL, pDayPlot, pDayPlotH,
                   pForPlotL, pForPlot, pForPlotH, nrow=2)
pDurPlot




# generate predictions for 4 quadrants of interest
willowPred <- willowNum %>% filter(id %in% c(25, 62, 150, 203)) %>%
  rename(elev2 = elevsq,
         forest2 = forestsq)
# predicting occurrence from the state process
predQuads <- modavgPred(list(mOptm), newdata = willowPred,
                        parm.type = "psi",
                        c.hat = gof.boot$c.hat.est)
willowRes <- willowPred %>% mutate(Predicted = predQuads$mod.avg.pred,
                                   SE = predQuads$uncond.se,
                                   lower = predQuads$lower.CL,
                                   upper = predQuads$upper.CL,
                                   elev = round((646.333*elev+1182.574),0),
                                   forest = forest*100) %>%
  select(-c(elev2, forest2, iLength, intensity1, intensity2, intensity3))












## APPENDIX PART 2: Testing Overfit Model Parameter Effects
#------------------------------------------------------------------------------#
#psi ~ elev | mean(forest)
pred_psi_eleL <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                       max(willowUnm@siteCovs$elev,
                                           na.rm=TRUE),
                                       length = 30),
                            forest = quantile(probs = 0.25,
                                              willowUnm@siteCovs$forest,
                                              na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
```

```r
predPsiEleL <- modavgPred(list(mOverpred), newdata = pred_psi_eleL,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleL <- pred_psi_eleL %>% mutate(Predicted = predPsiEleL$mod.avg.pred,
                                          SE = predPsiEleL$uncond.se,
                                          lower = predPsiEleL$lower.CL,
                                          upper = predPsiEleL$upper.CL,
                                          elevR = 1182.574 + elev*646.333)
ggpsieleL <- ggplot(data = pred_psi_eleL, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Elevation (m)") + ylim(0,1) + theme_bw()

pred_psi_eleM <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                       max(willowUnm@siteCovs$elev,
                                           na.rm=TRUE),
                                       length = 30),
                            forest = median(willowUnm@siteCovs$forest,
                                            na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiEleM <- modavgPred(list(mOverpred), newdata = pred_psi_eleM,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleM <- pred_psi_eleM %>% mutate(Predicted = predPsiEleM$mod.avg.pred,
                                          SE = predPsiEleM$uncond.se,
                                          lower = predPsiEleM$lower.CL,
                                          upper = predPsiEleM$upper.CL,
                                          elevR = 1182.574 + elev*646.333)
ggpsieleM <- ggplot(data = pred_psi_eleM, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Elevation (m)") + ylim(0,1) + theme_bw()

pred_psi_eleH <- data.frame(elev = seq(min(willowUnm@siteCovs$elev,
                                            na.rm=TRUE),
                                       max(willowUnm@siteCovs$elev,
                                           na.rm=TRUE),
                                       length = 30),
                            forest = quantile(probs = 0.75,
                                              willowUnm@siteCovs$forest,
                                              na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiEleH <- modavgPred(list(mOverpred), newdata = pred_psi_eleH,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_eleH <- pred_psi_eleH %>% mutate(Predicted = predPsiEleH$mod.avg.pred,
                                          SE = predPsiEleH$uncond.se,
                                          lower = predPsiEleH$lower.CL,
```

```r
                                            upper = predPsiEleH$upper.CL,
                                            elevR = 1182.574 + elev*646.333)
ggpsieleH <- ggplot(data = pred_psi_eleH, aes(x = elevR, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Elevation (m)") + ylim(0,1) + theme_bw()


#----------------------------------------------------------------------------#
#psi ~ for | mean(elev)
pred_psi_forL <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         max(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         length = 30),
                            elev = quantile(probs = 0.25,
                                            willowUnm@siteCovs$elev,
                                            na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForL <- modavgPred(list(mOverpred), newdata = pred_psi_forL,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_forL <- pred_psi_forL %>% mutate(Predicted = predPsiForL$mod.avg.pred,
                                          SE = predPsiForL$uncond.se,
                                          lower = predPsiForL$lower.CL,
                                          upper = predPsiForL$upper.CL,
                                          forestP = forest*100)
ggpsiforL <- ggplot(data = pred_psi_forL, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%)") + ylim(0,1) + theme_bw()


pred_psi_forM <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         max(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         length = 30),
                            elev = median(willowUnm@siteCovs$elev,
                                          na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForM <- modavgPred(list(mOverpred), newdata = pred_psi_forM,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_forM <- pred_psi_forM %>% mutate(Predicted = predPsiForM$mod.avg.pred,
                                          SE = predPsiForM$uncond.se,
                                          lower = predPsiForM$lower.CL,
                                          upper = predPsiForM$upper.CL,
                                          forestP = forest*100)
ggpsiforM <- ggplot(data = pred_psi_forM, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
```

```r
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%)") + ylim(0,1) + theme_bw()

pred_psi_forH <- data.frame(forest = seq(min(willowUnm@siteCovs$forest,
                                              na.rm=TRUE),
                                         max(willowUnm@siteCovs$forest,
                                             na.rm=TRUE),
                                         length = 30),
                            elev = quantile(probs = 0.75,
                                            willowUnm@siteCovs$elev,
                                            na.rm=TRUE)) %>%
  mutate(elev2 = elev^2,
         forest2 = forest^2)
predPsiForH <- modavgPred(list(mOverpred),
                          newdata = pred_psi_forH,
                          parm.type = "psi",
                          c.hat = gof.boot$c.hat.est)
pred_psi_forH <- pred_psi_forH %>% mutate(Predicted = predPsiForH$mod.avg.pred,
                                          SE = predPsiForH$uncond.se,
                                          lower = predPsiForH$lower.CL,
                                          upper = predPsiForH$upper.CL,
                                          forestP = forest*100)
ggpsiforH <- ggplot(data = pred_psi_forH, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#21918c", alpha=0.1) +
  geom_line(size=1,color="#21918c") +
  ylab("P(Occupied)") + xlab("Forest Cover (%)") + ylim(0,1) +
  theme_bw()

cowplot::plot_grid(ggpsieleL, ggpsieleM, ggpsieleH,
                   ggpsiforL, ggpsiforM, ggpsiforH, nrow=2)

#------------------------------------------------------------------------------#
#p ~ elev | median(day & forest & dur)
pred_p_elev <- data.frame(elev = seq(min(willowUnm@obsCovs$elev,
                                         na.rm=TRUE),
                                     max(willowUnm@obsCovs$elev,
                                         na.rm=TRUE),
                                     length = 30),
                          day = median(willowUnm@obsCovs$day, na.rm=TRUE),
                          forest = median(willowUnm@obsCovs$forest,
                                          na.rm=TRUE),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE))
predPEle <- modavgPred(list(mOverpred),
                       newdata = pred_p_elev,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_elev <- pred_p_elev %>% mutate(Predicted = predPEle$mod.avg.pred,
                                      SE = predPEle$uncond.se,
                                      lower = predPEle$lower.CL,
                                      upper = predPEle$upper.CL,
                                      forestP = forest*100)
```

```r
ggplot(data = pred_p_elev, aes(x = elev, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Elevation") + ylim(0,1) +
  theme_bw()
#---------------------------------------------------------------------------#
#p ~ dur | median(day & forest)
pred_p_dur <- data.frame(dur = seq(min(willowUnm@obsCovs$dur,
                                        na.rm=TRUE),
                                   max(willowUnm@obsCovs$dur,
                                       na.rm=TRUE),
                                   length = 30),
                         day = median(willowUnm@obsCovs$day, na.rm=TRUE),
                         forest = median(willowUnm@obsCovs$forest,
                                         na.rm=TRUE),
                         elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPDur <- modavgPred(list(mOverpred), newdata = pred_p_dur,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_dur <- pred_p_dur %>% mutate(Predicted = predPDur$mod.avg.pred,
                                    SE = predPDur$uncond.se,
                                    lower = predPDur$lower.CL,
                                    upper = predPDur$upper.CL,
                                    forestP = forest*100)
ggplot(data = pred_p_dur, aes(x = dur, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Survey Duration (min)") + ylim(0,1) +
  theme_bw()
#---------------------------------------------------------------------------#
#p ~ day | Q2(forest) + median(everything else)
pred_p_dayL <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                    max(willowUnm@obsCovs$day, na.rm=TRUE),
                                    length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          forest = quantile(probs = 0.25,
                                            willowUnm@obsCovs$forest,
                                            na.rm=TRUE),
                          elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPDayL <- modavgPred(list(mOverpred),
                        newdata = pred_p_dayL,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_dayL <- pred_p_dayL %>% mutate(Predicted = predPDayL$mod.avg.pred,
                                      SE = predPDayL$uncond.se,
                                      lower = predPDayL$lower.CL,
                                      upper = predPDayL$upper.CL,
                                      forestP = forest*100)
pDayPlotL <- ggplot(data = pred_p_dayL, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
```

```r
  ylab("P(Detected)") + xlab("Survey Day (8% Forested)") +
  ylim(0,1) +
  theme_bw()
#p ~ day | Q2(dur & forest)
pred_p_day <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                   max(willowUnm@obsCovs$day, na.rm=TRUE),
                                   length = 30),
                         dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                         forest = quantile(probs = 0.5,
                                           willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                         elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPDay <- modavgPred(list(mOverpred), newdata = pred_p_day,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_day <- pred_p_day %>% mutate(Predicted = predPDay$mod.avg.pred,
                                    SE = predPDay$uncond.se,
                                    lower = predPDay$lower.CL,
                                    upper = predPDay$upper.CL,
                                    forestP = forest*100)
pDayPlot <- ggplot(data = pred_p_day, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Survey Day (33% Forested)") + ylim(0,1) +
  theme_bw()
#p ~ day | Q4(forest) + median(everything else)
pred_p_dayH <- data.frame(day = seq(min(willowUnm@obsCovs$day, na.rm=TRUE),
                                    max(willowUnm@obsCovs$day, na.rm=TRUE),
                                    length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          forest = quantile(probs = 0.75,
                                            willowUnm@obsCovs$forest,
                                            na.rm=TRUE),
                          elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPDayH <- modavgPred(list(mOverpred), newdata = pred_p_dayH,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_dayH <- pred_p_dayH %>% mutate(Predicted = predPDayH$mod.avg.pred,
                                      SE = predPDayH$uncond.se,
                                      lower = predPDayH$lower.CL,
                                      upper = predPDayH$upper.CL,
                                      forestP = forest*100)
pDayPlotH <- ggplot(data = pred_p_dayH, aes(x = day, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") +
  xlab("Survey Day (57% Forested)") +
  ylim(0,1) +
  theme_bw()
#-----------------------------------------------------------------------#
#p ~ for | Q2(day), median(everything else)
```

```r
pred_p_forL <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                            na.rm=TRUE),
                                        max(willowUnm@obsCovs$forest,
                                            na.rm=TRUE),
                                        length = 30),
                          dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                          day = quantile(probs = 0.25,
                                         willowUnm@obsCovs$day,
                                         na.rm=TRUE),
                          elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPForL <- modavgPred(list(mOverpred), newdata = pred_p_forL,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_forL <- pred_p_forL %>% mutate(Predicted = predPForL$mod.avg.pred,
                                      SE = predPForL$uncond.se,
                                      lower = predPForL$lower.CL,
                                      upper = predPForL$upper.CL,
                                      forestP = forest*100)
pForPlotL <- ggplot(data = pred_p_forL, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 38") + ylim(0,1) +
  theme_bw()
#p ~ for | median(everything
pred_p_for <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                          na.rm=TRUE),
                                      max(willowUnm@obsCovs$forest,
                                          na.rm=TRUE),
                                      length = 30),
                         dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                         day = quantile(probs = 0.5,
                                        willowUnm@obsCovs$day,
                                        na.rm=TRUE),
                         elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPFor <- modavgPred(list(mOverpred), newdata = pred_p_for,
                       parm.type = "detect",
                       c.hat = gof.boot$c.hat.est)
pred_p_for <- pred_p_for %>% mutate(Predicted = predPFor$mod.avg.pred,
                                    SE = predPFor$uncond.se,
                                    lower = predPFor$lower.CL,
                                    upper = predPFor$upper.CL,
                                    forestP = forest*100)
pForPlot <- ggplot(data = pred_p_for, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 52") + ylim(0,1) +
  theme_bw()
#p ~ for | Q4(day), median(others)
pred_p_forH <- data.frame(forest = seq(min(willowUnm@obsCovs$forest,
                                           na.rm=TRUE),
                                       max(willowUnm@obsCovs$forest,
```

```r
                                                na.rm=TRUE),
                                length = 30),
                    dur = median(willowUnm@obsCovs$dur, na.rm=TRUE),
                    day = quantile(probs = 0.75, willowUnm@obsCovs$day,
                                   na.rm=TRUE),
                    elev = median(willowUnm@obsCovs$elev, na.rm=TRUE))
predPForH <- modavgPred(list(mOverpred), newdata = pred_p_forH,
                        parm.type = "detect",
                        c.hat = gof.boot$c.hat.est)
pred_p_forH <- pred_p_forH %>% mutate(Predicted = predPForH$mod.avg.pred,
                                      SE = predPForH$uncond.se,
                                      lower = predPForH$lower.CL,
                                      upper = predPForH$upper.CL,
                                      forestP = forest*100)
ggplot(data = pred_p_forH, aes(x = forestP, y = Predicted)) +
  geom_ribbon(aes(ymin=lower, ymax=upper), fill="#440154", alpha=0.1) +
  geom_line(size=1,color="#440154") +
  ylab("P(Detected)") + xlab("Forest (%) on Day 72") + ylim(0,1) +
  theme_bw()

# all together
cowplot::plot_grid(pDayPlotL, pDayPlot, pDayPlotH,
                   pForPlotL, pForPlot, pForPlotH, nrow=2)
```

References

1. Mollet, P., Zbinden, N. & Schmid, H. Steigende Bestandszahlen bei Spechten und anderen Vogelarten dank Zunahme von Totholz? | An increase in the population of woodpeckers and other bird species thanks to an increase in the quantities of deadwood? *Schweizerische Zeitschrift fur Forstwesen* **160**, 334–340 (2009).

2. Kumpula, S., Vatka, E., Orell, M. & Rytkönen, S. Effects of forest management on the spatial distribution of the willow tit (*Poecile montanus*). *Forest Ecology and Management* **529**, 120694 (2023).

3. Parry, W. & Broughton, R. K. Nesting behaviour and breeding success of Willow Tits Poecile montanus in north-west England. *Ringing & Migration* **33**, 75–85 (2018).

4. Knaus, P. *et al. Swiss Breeding Bird Atlas 2013–2016. Distribution and Population Trends of Birds in Switzerland and Liechtenstein.* (Swiss Ornithological Institute, Sempach, 2018).

5. Riecke, T. V., Gibson, D., Kéry, M. & Schaub, M. Sharing detection heterogeneity information among species in community models of occupancy and abundance can strengthen inference. *Ecology and Evolution* **11**, 18125–18135 (2021).

6. Bani, L., Luppi, M., Rocchia, E., Dondina, O. & Orioli, V. Winners and losers: How the elevational range of breeding birds on Alps has varied over the past four decades due to climate and habitat changes. *Ecology and Evolution* **9**, 1289–1305 (2019).

7. Sutherland, C. Statsecol: A Package Assocaited With The Statistical Ecology MSc. (2024).

8. Kellner, K. F. *et al.* The unmarked R package: Twelve years of advances in occurrence and abundance modelling in ecology. *Methods in Ecology and Evolution* **14**, 1408–1415 (2023).

9. R Core Team. R: A Language and Environment for Statistical Computing. (2023).

10. Bartón, K. MuMIn: Multi-Model Inference. (2023).

11. Akaike, H. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723 (1974).

12. Mazerolle, M. J. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). (2023).

13. Kéry, M. & Royle, J. A. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS.* vol. 1 (Elsevier/AP, Academic Press is an imprint of Elsevier, Amsterdam ; Boston, 2016).

14. Vanhinsbergh, D., Fuller, R. J. & Noble, D. *A Review of Possible Causes of Recent Changes in Populations of Woodland Birds in Britain.* (British Trust for Ornithology, Norfolk, 2003).

15. Rottler, E., Kormann, C., Francke, T. & Bronstert, A. Elevation-dependent warming in the Swiss Alps 1981–2017: Features, forcings and feedbacks. *International Journal of Climatology* **39**, 2556–2568 (2019).

16. HOHNSBEIN, J., PIEKARSKI, C., KAMPMANN, B. & NOACK, Th. Effects of heat on visual acuity. *Ergonomics* **27**, 1239–1246 (1984).

17. Cole, D. *Parameter Redundancy and Identifiability.* (Chapman; Hall/CRC, New York, 2020). doi:10.1201/9781315120003.

18. Szerencsits, E. Swiss tree lines - a GIS-based Approximation. *Landscape Online* 28–28 (2012) doi:10.3097/LO.201228.

19.   Vitasse, Y. *et al.* Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography* **39**, 1439–1449 (2012).