

The forestecology R package for modeling interspecies competition between trees

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Abstract

Move abstract below here after completed.

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Abstract (350 words)

1. When modeling growth of trees forest ecologists often incorporate the effect of interspecies competition. Many such models are based on a neighborhood effect assumption whereby all trees within a fixed distance of all focal trees are considered competitors. Methods are needed to evaluate the effect of interspecies competition and to assess their quality.
2. We present the `forestecology` package providing methods for both 1) evaluating the out-of-sample performance of our model using spatial-crossvalidation and 2) testing a null hypothesis of no impact of competitor species' identity on the growth of trees using a permutation test. We implement a class and methods using R's S3 object-oriented system, for a specific linear, Bayesian neighborhood competition model of tree growth.
3. We demonstrate the package's functions using data from the Smithsonian Conservation Biology Institute's large forest dynamics plot, part of the ForestGEO network of research sites. Given ForestGEO's data collection protocols and data formatting standards, the package cross-compatibility of code. We show both that 1) competitor species identity matters and 2) that not spatially cross-validating leads to error estimates that are overly optimistic.
4. The package follows `tidyverse`-like structure whereby verb-named functions can be modularly "piped" in sequence to intuitively display the sequence of steps of analysis from start to finish. Additionally, most inputs/outputs of functions assume an are of `sf` class from the simple features package, thereby facilitating all wrangling and visualization of geospatial data. Lastly, even though our package is currently limited to one specific model, the package is setup such that it can be easily extended to other models.

1 Introduction

Repeat-censused forest plots offer excellent data to test neighborhood models of tree competition Allen & Kim (2020) Canham et al. (2006) Uriarte et al. (2004). Here we describe

an R package, `forestecology`, to do that. This package implements the methods in Allen & Kim (2020). It provides: a convenient way to specify and fit models of tree growth based on neighborhood competition; a spatial cross validation method to test and compare model fits Roberts et al. (2017); and an ANOVA-like method to assess whether the competitor identity matters in these models. The model is written to work with ForestGEO plot data Anderson-Teixeira et al. (2015), but we envision that it could easily be modified to work with data from other forest plots, e.g. the US Forest Service Forest Inventory and Analysis plots Smith (2002).

The `forestecology` is designed with “tidy” data principles in mind as Wickham et al. (2019).

Given that our data is of geo-spatial nature, we represent our data using the “simple features” `sf` package class of objects Pebesma (2018) whereby. While previously the `sp` package serves such purposes Pebesma & Bivand (2005), the `sf` package is designed to interface with the `tidyverse` suite of packages.

1.1 Model for growth of tree

While there are a littany of models one can consider, in PLOSONe we considered a simple one.

Describe model specifics. Bayesian linear regression model.

Next we fit the following linear model to the DBH of each focal tree. Let $i = 1, \dots, n_j$ index all n_j trees of “focal” species group j ; let $j = 1, \dots, J$ index all J focal species groups; and let $k = 1, \dots, K$ index all K “competitor” species groups. We modeled the growth in diameter per year y_{ij} (in centimeters per year) of the i^{th} tree of focal species group j as a linear model f of the following covariates \vec{x}_{ij}

$$y_{ij} = f(\vec{x}_{ij}) + \epsilon_{ij} = \beta_{0,j} + \beta_{\text{DBH},j} \cdot \text{DBH}_{ij} + \sum_{k=1}^K \lambda_{jk} \cdot \text{BA}_{ijk} + \epsilon_{ij}$$

Link to <https://doi.org/10.1371/journal.pone.0229930.s004>

For this linear model’s case, there exists a closed form solution as described here. As such, the `fit_bayesian_model()` function using matrix algebra to obtain all parameter estimates, rather than computationally expensive Monte Carlo approximations. The inputs

to this function are a `focal_vs_comp` data frame, `prior_param` a list of priors, and a boolean flag `run_shuffle` on whether or not to run competitor-species identity permutations which we will demonstrate below on the Michigan Big Woods data. This function returns the posterior means of all parameters.

2 Example

We demonstrate the `forestecology` package's features on the Smithsonian Conservation Biology Institute (SCBI) large forest dynamics plot, located at the Smithsonian's National Zoo and Conservation Biology Institute in Front Royal, VA, USA. The 25.6 ha (640 x 400 m) plot is located at the intersection of three of the major physiographic provinces of the eastern US: the Blue Ridge, Ridge and Valley, and Piedmont provinces and is adjacent to the northern end of Shenandoah National Park. The forest type is typical mature secondary eastern mixed deciduous forest, with a canopy dominated by tulip poplar (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and hickories (*Carya* spp.), and an understory composed mainly of spicebush (*Lindera benzoin*), paw-paw (*Asimina triloba*), American hornbeam (*Carpinus caroliniana*), and witch hazel (*Hamamelis virginiana*) Bourg et al. (2013).

A high-level overview of the steps of our analysis pipeline is as follows:

1. Compute the growth of trees based on census data
2. Add spatial information:
 1. Define buffer region trees.
 2. Add spatial cross-validation block information.
3. Identify all focal and corresponding competitor trees.
4. Fit model, make predictions, and visualize model results

Additionally,

1. Evaluate the effect of competitor species identity using permutation tests.
2. Evaluate model performance using spatial cross-validation.

We load all necessary packages.

```
library(tidyverse)
library(lubridate)
library(sf)
library(forestecology)
library(blockCV)
library(patchwork)
```

2.1 Compute the growth of trees based on census data

The first step in our analysis sequence is to compute the growth of trees using data from two censuses. The `compute_growth()` function computes growth assuming census data that follows ForestGEO standards. Despite such standards, minor variations will still exist between sites thereby necessitating some data wrangling and checking. For example, the SCBI site records all DBH's in millimeters, whereas the Michigan Big Woods site records them in centimeters Anderson-Teixeira et al. (2015) Allen et al. (2020). The data format of other sites may be such that our `compute_growth()` function doesn't work at all. However, in the end all that matters is that the growth of all trees is saved in a data frame of class `sf` whereby the geolocation of each tree is presented in a `geometry` variable of type `<POINT>` and at a minimum the data contains the following variables: a variable uniquely identifying each tree-stem, `sp` of type `fct` factor identifying species, `dbh1` and `dbh2` of type `dbl` quantifying the DBH at earlier and later census, and `growth` of type `dbl` double quantifying the average annual growth in centimeters.

We load both 2008 and 2014 SCBI census data `.csv` files as they existed on GitHub on November 20, 2020. After selecting only relevant variables, we perform a few additional data wrangling steps: convert the variable with the date of measurement to be of type `date`, convert DBH to be in centimeters¹, convert the `sp` variable containing species information from type `chr` character to `fct` factor (we will discuss the need for this in Section 2.6). Furthermore, in order to speed up computation for purposes of this example, we only

¹A rule of thumb to determine the units of DBH is check if the smallest non-zero and non-missing measurement is 1 or 10. If the former, then centimeters. If the later, then millimeters. This is because ForestGEO protocols state that only trees with DBH greater or equal to 1cm should be included in censuses.

102 consider a 9 ha subsection of the 25.6 ha of the SCBI site: gx from 0–300 instead of 0–400
103 and gy from 300–600 instead of 0–640.

```
census_2013_scbi <- read_csv("scbi.stem2.csv") %>%  
  select(stemID, sp, date = ExactDate, gx, gy, dbh, codes, status) %>%  
  mutate(  
    date = mdy(date),  
    dbh = as.numeric(dbh)/10,  
    sp = factor(sp)  
  ) %>%  
  filter(gx < 300, between(gy, 300, 600))  
  
census_2018_scbi <- read_csv("scbi.stem3.csv") %>%  
  select(stemID, sp, date = ExactDate, gx, gy, dbh, codes, status) %>%  
  mutate(  
    date = mdy(date),  
    dbh = as.numeric(dbh)/10,  
    sp = factor(sp)  
  ) %>%  
  filter(gx < 300, between(gy, 300, 600))
```

104 These two data frames are then used as the two primary arguments to the `compute_growth()`
105 function, along with the `id` argument whereby the user specifies the name of the variable
106 that uniquely identifies each tree-stem under consideration (note this does not include
107 resprouts in the later census):

```
growth_scbi <-  
  compute_growth(  
    census_1 = census_2013_scbi,  
    census_2 = census_2018_scbi %>% filter(!str_detect(codes, "R")),  
    id = "stemID"  
  )
```

```

growth_scbi
## Simple feature collection with 7954 features and 8 fields
## geometry type:  POINT
## dimension:      XY
## bbox:           xmin: 0.2 ymin: 300 xmax: 299.9 ymax: 600
## CRS:            NA
## # A tibble: 7,954 x 9
##   stemID sp      dbh1 codes1 status  dbh2 codes2 growth    geometry
##   <dbl> <fct> <dbl> <chr>  <chr>  <dbl> <chr>  <dbl>    <POINT>
## 1      4 nysy  13.6  M      A      14.2 M      0.103 (14.2 428.5)
## 2      5 havi   8.8  M      A       9.6 M;P    0.150 (9.4 436.4)
## 3      6 havi   3.25 NULL  A       4      M    0.140 (1.3 434)
## 4     77 qual  65.2  M      A      66      M    0.141 (34.7 307.2)
## 5     79 tiam  47.7  M      A     46.8 M    -0.161 (40 381.1)
## # ... with 7,949 more rows

```

The output `growth_scbi` is a single data frame of class `sf` that includes a numerical `growth` reflecting the average annual growth in DBH (in cm) for all trees that were alive at both time points as well a `geometry` variable encoding each tree's geolocation. Furthermore, variables that (in theory) remain unchanged between censuses appear only once, such as location variables `gx` and `gy`; as well as species-related variables. Variables that should change between censuses are suffixed with 1 and 2 indicating the earlier and later censuses, such as `dbh1/dbh2` and `codes1/codes2`.

Given that `growth_scbi` is of class `sf`, it can be easily plotted in `ggplot2` using the `geom_sf()` geometry as seen in Figure 1.

TODO: Rescale points in this plot:

```

ggplot() +
  geom_sf(data = growth_scbi, aes(size = growth)) +
  scale_size(breaks = c(0.01, 0.1, 1), range = c(0.1, 1))

```

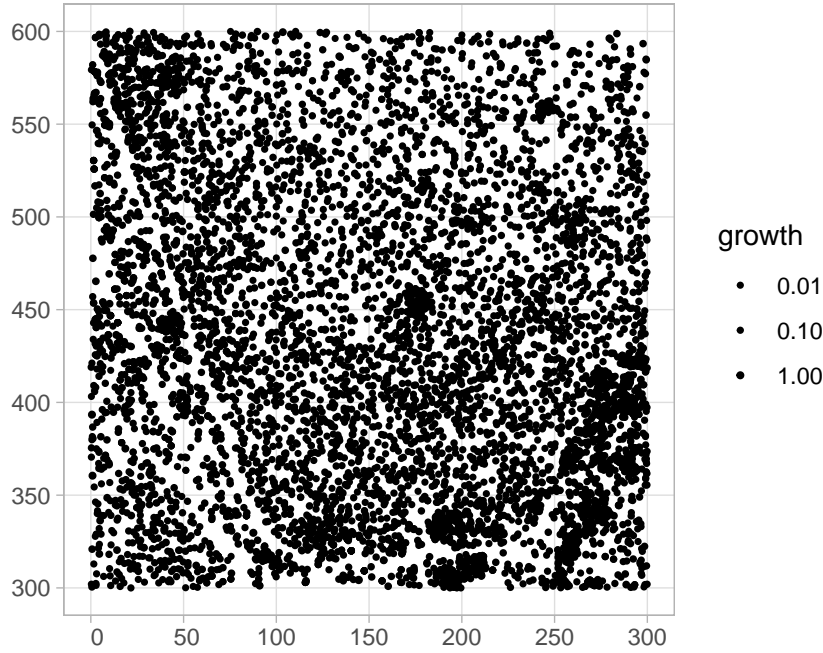


Figure 1: Growth of trees at SCBI.

2.2 Add spatial information

The next step in our analysis sequence is to add spatial information to our main `growth_scbi` data frame. The first element of spatial information we add is a “buffer region” to the periphery of the study region. Since some of our model’s explanatory variables such as competitor basal area are cumulative, we must ensure that all trees being modeled are not biased to have different neighbor structures. This is of particular concern for trees at the boundary of study regions, which will not have the same number of neighbors that act as competitors as trees in the internal part of the study region. In order to account for such edge effects only trees who are not part of this buffer region, i.e. are part of the interior of the study region, will have their growths modeled Waller & Gotway (2004).

Our model of interspecific competition relies on a spatial definition of who the competitor trees are for focal trees of interest: all trees within a distance `comp_dist` of a focal tree are considered its competitors (assuming the same units as the `gx` and `gy` location variables). In our case we set this value below at 7.5m, a value informed by Canham et al. (2004) Uriarte et al. (2004) Canham et al. (2006). Using this value along with a manually constructed `sf` object representation of the study region’s boundary, we apply the

134 `add_buffer_variable()` to our `growth_scbi` data frame to add a `buffer` boolean variable:
135 all trees who have `buffer` set to `FALSE` will be our focal trees whose growths are modeled,
136 whereas those with `buffer` set to `TRUE` will only be considered as competitor trees whose
137 growth will not be modeled.

```
# Define buffer region using competitive distance range
comp_dist <- 7.5

study_region_scbi <- tibble(
  x = c(0, 300, 300, 0, 0),
  y = c(300, 300, 600, 600, 300)
) %>%
  sf_polygon()

growth_scbi <- growth_scbi %>%
  add_buffer_variable(size = comp_dist, region = study_region_scbi)
```

138 The second element of spatial information are blocks corresponding to folds of a spatial
139 cross-validation algorithm used to estimate model error. Conventional cross-validation
140 algorithms assign observations to folds by randomly resampling individual observations.
141 However, underlying this algorithm is an assumption that the observations are independent.
142 In the case of forest census data, observations exhibit spatial autocorrelation. This spatial
143 dependence is incorporated into the cross-validation algorithm by randomly resampling
144 spatial blocks of trees Roberts et al. (2017) Pohjankukka et al. (2017). We therefore
145 associate each observed tree to one of k spatial folds. In the example below, we first
146 manually define two folds that partition the study region as an `sf` object. We then use
147 the output of the `spatialBlock()` function from the `blockCV` package to associate each
148 tree in `growth_scbi` to the correct fold (saved in the `foldID` variable) Valavi et al. (2019).
149 \footnote{In the Appendix we present an example where the folds themselves are also
150 created using the `spatialBlock()` function given a specified `cv_block_size`.}

```

# Manually define spatial blocks to act as folds
fold1 <- rbind(c(0, 300), c(150, 300), c(150, 600), c(0, 600))
fold2 <- rbind(c(150, 300), c(300, 300), c(300, 600), c(150, 600))

blocks_scbi <- bind_rows(sf_polygon(fold1), sf_polygon(fold2)) %>%
  mutate(folds = c(1, 2) %>% factor())

# Associate each observation to a fold
SpatialBlock_scbi <- spatialBlock(
  speciesData = growth_scbi, k = 2, selection = "systematic",
  blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE
)

growth_scbi <- growth_scbi %>%
  mutate(foldID = SpatialBlock_scbi$foldID %>% factor())

```

151 Figure 2 illustrates the net effect of adding these two elements of information to the
 152 `growth_scbi` data frame. The location of each tree is marked with an integer indicating
 153 which fold it belongs to, where the folds are marked with solid lines. The color of each digit
 154 indicates whether the tree is part of the buffer region (and thus will only be considered as
 155 a competitor tree in our model) or is part of the interior of the study region (and thus is a
 156 focal tree whose growth is of modeled interest).

```

ggplot() +
  geom_sf_text(data = growth_scbi, aes(label = foldID, col = buffer), alpha = 0.2) +
  geom_sf(data = blocks_scbi, fill = "transparent")

```

157 TODO: Do we talk about `add_buffer_variable(direction = "out")` when each fold
 158 gets its turn being the training data?

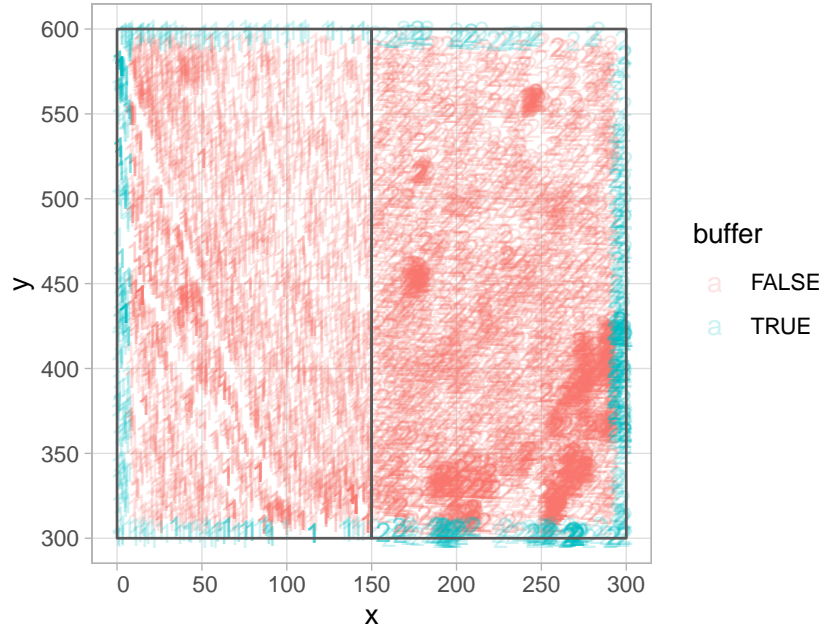


Figure 2: Buffer region and cross-validation block information for SCBI data.

2.3 Identify all focal and corresponding competitor trees

The next step in our analysis sequence is to identify all focal trees and their corresponding competitor trees. The `create_focal_vs_comp()` function performs these tasks and returns a new data frame of type `sf` containing this information. On top of the previously discussed arguments `comp_dist` defining the competition neighborhood and `id` indicating which variable in the data frame uniquely identifies each tree-stem, this function also requires an `sf` object representation of the spatial cross-validation blocks/folds; in our case, this was manually encoded in the `blocks_scbi` in Section 2.2 while in our Appendix we present an example where this was performed using `spatialBlock()` from the `blockCV` package. We present the resulting data frame below with the `foldID` variable omitted for compactness of presentation.

```
focal_vs_comp_scbi <- growth_scbi %>%
  create_focal_vs_comp(comp_dist, cv_grid_sf = blocks_scbi, id = "stemID")
focal_vs_comp_scbi %>%
  select(-foldID)
## # A tibble: 6,296 x 6
```

```
##   focal_ID focal_sp   dbh      geometry growth comp
##      <dbl> <fct>    <dbl>      <POINT>  <dbl> <list>
## 1         4 nysy     13.6 (14.2 428.5)  0.103 <tibble [20 x 4]>
## 2         5 havi      8.8 (9.4 436.4)  0.150 <tibble [32 x 4]>
## 3        79 tiam     47.7 (40 381.1) -0.161 <tibble [20 x 4]>
## 4        80 caca      5.15 (38.7 421.7)  0.253 <tibble [12 x 4]>
## 5        96 libe      2.3   (60 310)  0.262 <tibble [14 x 4]>
## # ... with 6,291 more rows
```

170 TODO: Below reconcile the number of rows as they off by one from `growth_scbi` pipe
 171 `filter(!is.na(growth) & !buffer)`. perhaps by removing NA's in the `growth_scbi`
 172 stage.

173 The resulting data frame `focal_vs_comp_scbi` has 6296 rows, representing the subset
 174 of the 7954 trees in `growth_scbi` that will be considered as focal trees and thus have their
 175 growths modeled. Recall from Section 2.2 this consists all trees that are not part of the
 176 buffer region in Figure 2. Two new variables `focal_ID` and `focal_sp` related to tree-stem
 177 identification and species information. Most notably however is a new variable `comp` which
 178 contains information on all competitor trees for a given focal tree saved in list-column
 179 format, a feature of the `tidyr` package Wickham (2020). For example, we drill-down on
 180 the tree with `focal_ID` equal to 4. It has 20 competitor trees each described by 4 variables
 181 as indicated by the fact that `comp` is a `<tibble [20 × 4]>`.

```
focal_vs_comp_scbi %>%
  filter(focal_ID == 4) %>%
  select(focal_ID, dbh, comp)
## # A tibble: 1 x 3
##   focal_ID   dbh comp
##     <dbl> <dbl> <list>
## 1         4 13.6 <tibble [20 x 4]>
```

182 Using the `unnest()` function from the `tidyr` package, we can flatten list-column into
 183 regular columns. We observe that for the same focal tree with DBH equal to 13.65cm, we

184 have information on all 20 competitor trees whose `dist` distance to the focal tree is less
 185 than or equal to 7.5, including their unique tree-stem ID number, their species, and their
 186 basal area (in m²) calculated as $\frac{\pi \times (DBH/2)^2}{10000}$ where *DBH* is the value from the earlier census
 187 in cm. Saving our focal versus competitor information in list-column minimizes redundancy
 188 since we do not repeat information on the focal tree 20 times.

```
focal_vs_comp_scbi %>%
  filter(focal_ID == 4) %>%
  select(focal_ID, dbh, comp) %>%
  unnest(cols = "comp")
```

```
189 ## # A tibble: 20 x 6
190 ##   focal_ID    dbh comp_ID    dist comp_sp comp_basal_area
191 ##   <dbl> <dbl>   <dbl> <dbl> <fct>         <dbl>
192 ## 1       4  13.6   1836  7.48 tiam          0.0176
193 ## 2       4  13.6   1847  2.81 nysy          0.00332
194 ## 3       4  13.6   1848  1.62 nysy          0.00396
195 ## 4       4  13.6   1849  2.62 nysy          0.00535
196 ## 5       4  13.6   1850  2.98 havi          0.00472
197 ## # ... with 15 more rows
```

198 2.4 Fit model and make predictions

199 Now that we've identified all focal and corresponding competitor trees and saved this
 200 information in a data frame of type `focal_vs_comp`, the next step in our analysis sequence
 201 is to fit a model for the growth of all focal trees. Currently the `forestecology` package can
 202 only fit the competition Bayesian linear regression model outlined in Section 1.1 using the
 203 `comp_bayes_lm()` function. However, any model implemented in a function that similarly
 204 takes an input data frame of type `focal_vs_comp` as an argument can be easily swapped
 205 in. In the case of our specific competition Bayesian linear regression model, we can also
 206 specify prior distributions on all parameters of interest (here chosen to be the defaults).

```
comp_bayes_lm_scbi <- focal_vs_comp_scbi %>%
  comp_bayes_lm(prior_param = NULL)
```

207 The returned `comp_bayes_lm_scbi` output is an object of S3 class type `comp_bayes_lm`
 208 which contains the posterior values of all parameters in our competition Bayesian lin-
 209 ear regression. This class of object includes generic methods implemented for `print()`,
 210 `predict()`, and `ggplot2::autoplot()`. First the generic for `print()` displays the names
 211 of all prior & posterior parameters (accessible via `comp_bayes_lm_scbi$prior_params` and
 212 `comp_bayes_lm_scbi$post_params`) along with the model formula:

```
comp_bayes_lm_scbi
## Bayesian linear regression model parameters with a multivariate Normal likelihood.
##
##   parameter_type          prior posterior
## 1 Inverse-Gamma on sigma^2 a_0    a_star
## 2 Inverse-Gamma on sigma^2 b_0    b_star
## 3 Multivariate t on beta   mu_0    mu_star
## 4 Multivariate t on beta   V_0     V_star
##
## Model formula:
## growth ~ sp + dbh + dbh * sp + acne * sp + acpl * sp + acru * sp + acsp * sp + aial
```

213 Next, the generic for `predict()` takes as inputs the posterior parameter values in
 214 `comp_bayes_lm_scbi` and the predictor variables in `newdata` and outputs a vector of fit-
 215 ted/predicted values \hat{y} of the DBH for each focal tree (as returned by the posterior predictive
 216 distribution).

```
focal_vs_comp_scbi <- focal_vs_comp_scbi %>%
  mutate(growth_hat = predict(comp_bayes_lm_scbi, newdata = focal_vs_comp_scbi))
```

```
focal_vs_comp_scbi
## # A tibble: 6,296 x 8
##   focal_ID focal_sp   dbh foldID      geometry growth
##   <dbl> <fct>   <dbl> <fct>   <POINT>   <dbl>
## 1         4 nysy    13.6  1      (14.2 428.5) 0.103
## 2         5 havi     8.8  1      (9.4 436.4) 0.150
## 3        79 tiam    47.7  1      (40 381.1) -0.161
## 4        80 caca     5.15  1      (38.7 421.7) 0.253
## 5        96 libe     2.3  1      (60 310) 0.262
## 6       101 litu    65.4  1      (47.1 567.3) 0.552
## 7       102 astr     1.99  1      (40.8 575.5) 0.0954
## 8       126 cato    37.4  1      (60.6 400.2) 0.165
## 9       127 caca     8.72  1      (72.7 514.1) 0.0370
## 10      139 astr     1.71  1      (96.7 315.1) 0.0549
## # ... with 6,286 more rows, and 2 more variables: comp <list>,
## #   growth_hat <dbl>
```

217 We can then compare the observed and fitted/predicted growths to compute the root
 218 mean squared error of our model fit.

```
model_rmse <- focal_vs_comp_scbi %>%
  rmse(truth = growth, estimate = growth_hat) %>%
  pull(.estimate)
model_rmse
## [1] 0.1281398
```

219 Lastly, the generic for `ggplot2::autoplot()` allows us to

```
# Plot posteriors for only a subset of species
sp_to_plot <- c("quru", "litu", "cagl", "cato")

plot1 <- autoplot(comp_bayes_lm_scbi, type = "intercepts", sp_to_plot = sp_to_plot)
```

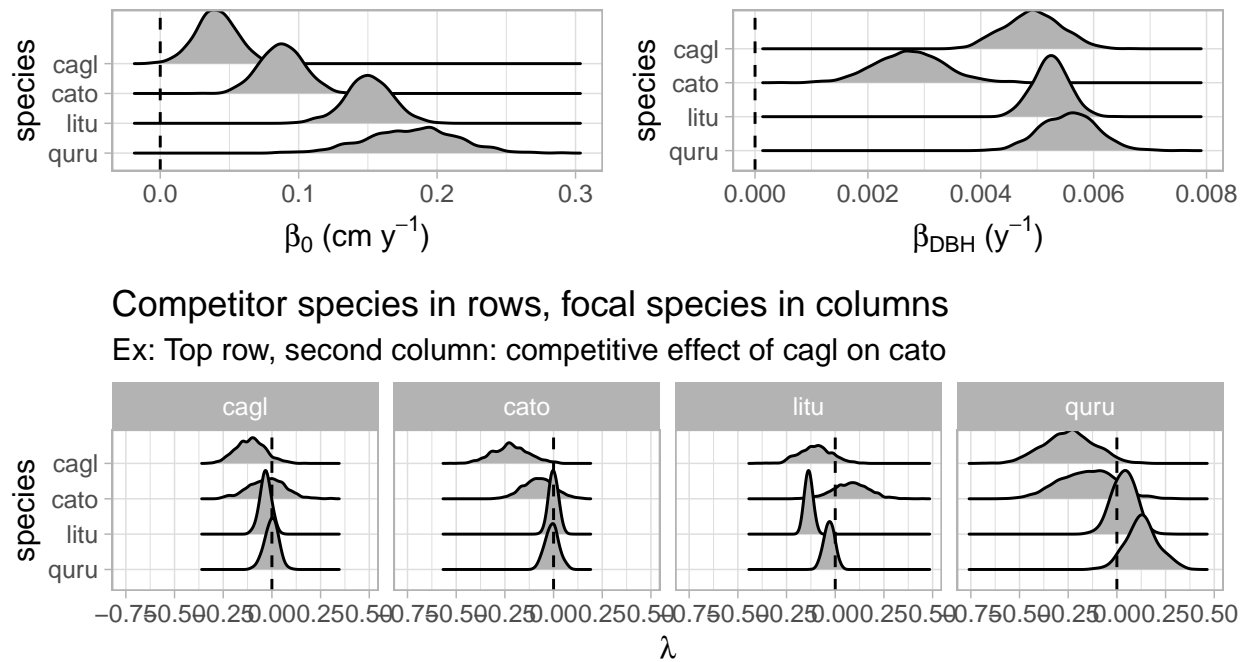


Figure 3: Posterior distributions of all parameters for a subset of species.

```
plot2 <- autoplot(comp_bayes_lm_scbi, type = "dbh_slopes", sp_to_plot = sp_to_plot)
plot3 <- autoplot(comp_bayes_lm_scbi, type = "competition", sp_to_plot = sp_to_plot)

# Combine plots using patchwork
(plot1 | plot2) / plot3
```

2.5 Evaluate the effect of competitor species identity using permutation tests

HEY BERT PICK IT UP HERE

```
comp_bayes_lm_scbi <- focal_vs_comp_scbi %>%
  comp_bayes_lm(prior_param = NULL, run_shuffle = TRUE)

focal_vs_comp_scbi <- focal_vs_comp_scbi %>%
  mutate(
```



```

    growth_hat = predict(comp_bayes_lm_scbi, newdata = focal_vs_comp_scbi)
  )

model_rmse <- focal_vs_comp_scbi %>%
  rmse(truth = growth, estimate = growth_hat) %>%
  pull(.estimate)
model_rmse

```

2.6 Evaluate model performance using spatial cross-validation

The model fits and predictions in Section 2.4 all suffer from a common failing: they use the same data to both fit the model and to assess the model's performance using the RMSE. As argued by Roberts et al. (2017), this can lead to overly optimistic assessments of model quality as the models can be overfit, in particular in situations where spatial-autocorrelation is present. To mitigate the effects of such overfitting, we use a spatially block cross-validation algorithm implemented in the `run_cv()`. This function at its core uses the same model fitting implemented in the `fit_bayesian_model()` function, however trains the model on $k - 1$ spatial folds of the train and returns fitted values for the test data. Recall that the spatial blocking scheme was encoded in Section 2.2.

Observe once again that this RMSE is much higher than that for the above SCBI model fit without cross-validation.

```

focal_vs_comp_scbi <- focal_vs_comp_scbi %>%
  run_cv(comp_dist = comp_dist, cv_grid = blocks_scbi)

focal_vs_comp_scbi %>%
  rmse(truth = growth, estimate = growth_hat) %>%
  pull(.estimate)
## [1] 0.1446232

```

3 Discussion

4 Acknowledgments

References

Allen, D., Dick, C., Burnham, R. J., Perfecto, I. & Vandermeer, J. (2020), ‘The michigan big woods research plot at the edwin s. george, pinckney, mi, usa’, *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **207**.

URL: <http://hdl.handle.net/2027.42/156251>

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