The forestecology R package for fitting and assessing models of interspecies competitive effects on the growth of trees

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Abstract

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- 1. Many models for the growth of trees that incorporate interspecies competition are based on a neighborhood effect assumption whereby all trees within a fixed distance of a focal tree are considered competitors. Methods and tools are needed to quantify this competitive effect and assess the quality of all resulting models.
- 2. We present the forestecology package providing methods for both 1) evaluating the effect of competitor species identity using permutation tests and 2) evaluating model performance using spatial cross-validation. Following Allen & Kim (2020), we implement a Bayesian linear regression competition model.
- 3. We demonstrate the package's functionality using data from the Smithsonian Conservation Biology Institute's large forest dynamics plot, part of the ForestGEO global network of reseach sites. Given ForestGEO's data collection protocols and data formatting standards, the package was designed with cross-site compatibility in mind. We demonstrate that both 1) competitor species identity matters and 2) that not spatially cross-validating leads to error estimates that are overly optimistic.
- 4. The package features 1) tidyverse-like structure whereby verb-named functions can be modularly "piped" in sequence, 2) functions with standardized inputs/outputs of simple features sf package class, and 3) an S3 object-oriented implementation of the Bayesian linear regression model. These three facts allow for clear articulation of all the steps in the sequence of analysis and easy wrangling and visualization of the

- geospatial forestry data. Furthermore, while the package only has Bayesian linear regression implemented, the package was designed with extensibility to other methods in mind.
- 29 Keywords: forest ecology, competition, R, Rstats, tidyverse, sf, cross-validation, spatial 30 statistics

1 Introduction

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BERT: Dave could you write a few sentences (and add references where appropriate) starting with the big picture of modeling tree growth, zooming in to neighborhood models, and 33 then connecting to the "Allen & Kim (2020) considers the following model" I write below? 34 Repeat-censused forest plots offer excellent data to test neighborhood models of the 35 effect of competition on the growth of trees Canham et al. (2006) Uriarte et al. (2004). 36 Allen & Kim (2020) considers the following model: Let $i = 1, ..., n_j$ index all n_j 37 trees of "focal" species group j; let j = 1, ..., J index all J focal species groups; and 38 let k = 1, ..., K index all K "competitor" species groups. We model the average annual growth in diameter y_{ij} (in centimeters per year) of the i^{th} tree of focal species group j as 40 a linear model f of the covariates \vec{x}_{ij}

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

where $\beta_{0,j}$ is the diameter-independent growth rate for group j; dbh_{ij} is the diameter at 42 breast height (in centimeters) of the focal tree at the earlier census; $\beta_{\text{dbh},j}$ is the amount of 43 the growth rate changed depending on diameter for group j; BA_{ijk} is the sum of the basal area of all trees of competitor species group k; λ_{jk} is the change in growth for individuals of group j from nearby competitors of group k; and ϵ_{ij} is a random error term distributed 46 Normal $(0, \sigma^2)$. They estimate all parameters via Bayesian linear regression while exploiting Normal/Inverse Gamma conjugacy to derive closed-form solutions to all posterior distribu-48 tions via linear algebra¹. These closed-form solutions for the posterior distributions are in 49 contrast to approximations of all posteriors via computationally expensive Markov Chain 50 Monte Carlo algorithms. 51

In order to evaluate whether competitor species identity matters, Allen & Kim (2020)

 $^{^1\}mathrm{See}$ S1 Appendix of Allen & Kim (2020), available at https://doi.org/10.1371/journal.pone.0229930.s004

run a permutation test where under the null hypothesis the species identity of all competitors of a focal tree can be permuted/shuffled:

$$H_0: \lambda_{jk} = \lambda_j \text{ for all } k = 1, \dots, K$$
 (2)

vs.
$$H_A$$
: at least one λ_{jk} is different (3)

where the null hypothesis H_0 reflects a hypothesis of no species grouping-specific ef-55 fects of competition while the alternative hypothesis H_A reflects a hypothesis of species 56 grouping-specific effects of competition. Furthermore, in order to account for the spatial 57 autocorrelation inherent to forest data in their estimates of out-of-sample model error, 58 Allen & Kim (2020) use spatial cross-validation. Estimates of model error that do not 59 account for this spatial dependency tend to underestiamte the true model error (Roberts 60 et al. 2017). 61 We introduce the forestecology R package providing methods and data for forest 62 ecology model fitting and assessment, available on CRAN (https://cran.r-project.org/ 63 web/packages/forestecology/index.html) with the corresponding source code available 64 on GitHub (https://github.com/rudeboybert/forestecology). The package implements all aspects of the model in Equation 1: model fitting and generating fitted/predicted values, evaluating the effect of competitor species identity using permutation tests, and 67 evaluating model performance using spatial cross-validation. 68 The package designed with "tidy" design principles in mind (Wickham et al. 2019). 69 Much like many of the tidyverse component packages, forestecology is designed with 70 verb-named functions that can be modularly composed in sequence using the pipe %>% 71 operator (Bache & Wickham 2020). As we articulate in Section 2, these functions delineate the key steps in our analysis sequence. Furthermore, the inputs and outputs of nearly all of our functions use the same "simple features for R" data structures as implemented in

the sf package for standardized support for spatial vector data (Pebesma 2018). The sf package is a tidyverse-friendly evolution of the sp package of classes and methods for spatial data in R (Pebesma & Bivand 2005). As such, wrangling and visualization spatial data such as ours becomes much easier.

Currently the package only implements the Bayesian linear regression model of tree 79 growth based on neighborhood competition detailed in Equation 1. As we demonstrate in Section 2.4 however, the fitting of this model is self-contained in a single function 81 comp_bayes_lm(). This function returns an object of S3 class type comp_bayes_lm with generic methods implemented for print() to inspect the output, predict() to generate fitted/predicted values, and ggplot2::autoplot() to visualize all results. Therefore the package can be modularly extended to fit other models as long as they are coded into a 85 function similar type as comp_bayes_lm() as has equivalent generic methods implemented. 86 We present a case-study of the forestecology package's use on data from the Smith-87 sonian Conservation Biology Institute's (SCBI) large forest dynamics plot in Front Royal, 88 Virginia, USA in Section 2, which is part of the ForestGEO global network of research 89 sites (Bourg et al. 2013, Anderson-Teixeira et al. (2015)). The package is designed with ForestGEO plot data in mind, 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 or more generally to model interactions of any community of mapped sessile organisms (Smith 2002).

95 2 forestecology workflow: a case study

We demonstrate the forestecology package's functionality on data from 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 (Bourg et al. 2013). 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).

The forestecology package has the following ecological goals: 1) to evaluate the effect of competitor species identity using permutation tests and 2) to evaluate model performance using spatial cross-validation. To achieve these goals, we outline a basic analysis sequence comprising of these four main steps:

- 1. Compute the growth of stems based on two censuses.
- 2. Add spatial information:
 - 1. Define a buffer region of trees.
 - 2. Add spatial cross-validation block information.
- 3. Identify all focal trees and their competitors.
- 4. Apply model, which includes:
 - 1. Fit model.

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- 2. Compute fitted/predicted values.
 - 3. Visualize posterior distributions.
- We start by loading all necessary packages.

```
library(tidyverse)
library(lubridate)
library(sf)
```

```
library(patchwork)
library(forestecology)
library(blockCV)
```

2.1 Step 1: Compute the growth of trees based on census data

The first step in the our analysis sequence is to compute the growth of trees using data from two censuses. The compute_growth() function computes average annual growth assuming census data that roughly 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 diameters at breast height (DBH) in millimeters (Bourg et al. 2013), whereas the Michigan Big Woods site records them in centimeters (Allen et al. 2020).

We load both 2008 and 2014 SCBI census data .csv files as they existed on GitHub on

We load both 2008 and 2014 SCBI census data .csv files as they existed on GitHub on
November 20, 2020. After selecting only the relevant variables, we perform a few additional
data wrangling steps: convert the character variable with the date of measurement to be
of explicit type date, convert DBH to be in centimeters² Furthermore, in order to speed
up computation for purposes of this example, we only consider a 9 ha subsection of the
25.6 ha of the SCBI site: gx from 0–300 instead of 0–400 and gy from 300–600 instead of

```
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
```

²A rule of thumb to determine the units of DBH is to 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.

```
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
) %>%
  filter(gx < 300, between(gy, 300, 600))</pre>
```

These two data frames are then supplied as arguments to the compute_growth() function, along with the id argument that specifies the variable that uniquely identifies each
tree-stem. Note furthermore that we discard all resprouts in the later census (those with
code == R), since we are only interested in the diameter growth of surviving, and not
resprouted, stems.

```
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: 300 ymax: 600
```

```
## CRS:
                      NA
## # A tibble: 7,954 x 9
                                             dbh2 codes2 growth
##
     stemID sp
                      dbh1 codes1 status
                                                                      geometry
       <dbl> <fct> <dbl> <chr>
                                    <chr>
                                            <dbl> <chr>
                                                             <db1>
                                                                       <POINT>
## 1
                     13.6
                                             14.2 M
                                                            0.103 (14.2 428)
           4 nysy
                                    Α
                                              9.6 M;P
## 2
           5 havi
                      8.8
                                                            0.150
                                                                     (9.4 436)
## 3
           6 havi
                      3.25 NULL
                                    \boldsymbol{A}
                                                             0.140
                                                                     (1.3 434)
## 4
          77 qual
                     65.2
                                             66
                                                             0.141 (34.7 307)
                                    \boldsymbol{A}
          79 tiam
                    47.7
                                             46.8 M
                                                           -0.161
                                                                      (40 381)
                                    Α
         with 7,949 more rows
```

The output growth_scbi is a single data frame of class sf that includes variables growth, the average annual growth in DBH (cm y⁻¹) for all stems that were alive at both time points, and geometry, the sf package's encoding of geolocations of type <POINT>. In addition the species variable sp is converted to a factor if it wasn't already by compute_growth().³ Furthermore, the variables that should 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.

Site data that does not align with this convention will need to be transformed for use with the compute_growth() function. However, in the end, all that matters is that the growth of all stems is saved in a data frame of class sf and, at a minimum, contains the variable uniquely identifying each stem, sp, dbh1, growth, geometry.

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 where we plot a random sample of 500 out of the

³In our spatial cross-validation algorithm in Section 2.6 issues can occur when rare species do not occur in the training set, but then are encountered in the test set. This risk is mitigated by representing sp as a factor variable, which has a complete list of all levels of the categorical variable.

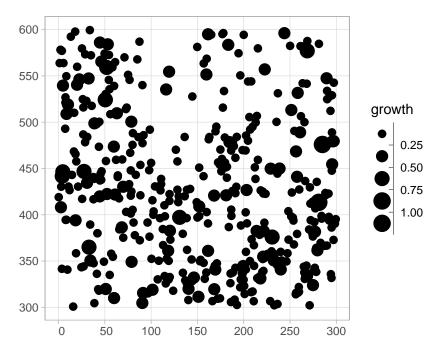


Figure 1: Compute growth of trees based on census data: Map with growth of a random sample of 500 trees from a 9 ha subsection of the Smithsonian Conservation Biology Institute (SCBI) forest plot.

155 7954 trees.

```
ggplot() +
geom_sf(data = growth_scbi %>% sample_n(500), aes(size = growth)) +
scale_size_binned(limits = c(0.1, 1))
```

2.2 Step 2: Add spatial information

The next step in our analysis sequence is to add additional 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 are cumulative (such as competitor basal area), we must ensure that all trees being modeled are not biased to have different neighbor structures. This is of concern for trees at the boundary of study regions, for which all neighbors will not be included in the censused

stems. In order to account for such edge effects, only trees that are not part of this buffer region, i.e. are part of the interior of the study region, will have their growth modeled (Waller & Gotway 2004).

Our model of interspecific competition relies on a spatial definition of who the competi-166 tor trees are for focal trees of interest: all trees within a distance comp_dist of a focal tree 167 are considered its competitors (assuming the same units as the gx and gy location vari-168 ables). In our case we set this value at 7.5m, a value informed by other studies (Canham et al. 2004, Uriarte et al. (2004), Canham et al. (2006)). Using this value along with a man-170 ually constructed sf object representation of the study region's boundary via its vertices, 171 we apply the add_buffer_variable() to our growth_scbi data frame to add a buffer 172 boolean variable: all trees who have buffer set to FALSE will be our focal trees whose 173 growth will be modeled, whereas those with TRUE will only be considered as competitor 174 trees whose growth will not.

```
# 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)
```

The second element of spatial information are blocks corresponding to folds of a spatial cross-validation algorithm used to estimate out-of-sample model error. Conventional cross-validation algorithms assign observations to folds by randomly resampling individual observations. However, many of these algorithms assume that the observations are
independent of each other. In the case of forest census data, observations exhibit spatial
autocorrelation. We therefore incorporate this spatial dependence into the cross-validation
algorithm with our spatial blocks of trees (Roberts et al. 2017, Pohjankukka et al. (2017))
In the example below, we first manually define four folds that partition the study region as
an sf object. We then use the output of the spatialBlock() function from the blockCV
package to associate each tree in growth_scbi to the correct fold (saved in the foldID
variable) (Valavi et al. 2019). 4

```
# Manually define spatial blocks to act as folds
n_fold <- 4

fold1 <- rbind(c(0, 300), c(150, 300), c(150, 450), c(0, 450))

fold2 <- rbind(c(150, 300), c(300, 300), c(300, 450), c(150, 450))

fold3 <- rbind(c(0, 450), c(150, 450), c(150, 600), c(0, 600))

fold4 <- rbind(c(150, 450), c(300, 450), c(300, 600), c(150, 600))

blocks_scbi <- bind_rows(
    sf_polygon(fold1), sf_polygon(fold2), sf_polygon(fold3), sf_polygon(fold4))

%%

mutate(folds = c(1:n_fold) %>% factor())

# Associate each observation to a fold

spatial_block_scbi <- spatialBlock(
    speciesData = growth_scbi, k = n_fold, selection = "systematic",
    blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE</pre>
```

⁴In the Appendix we present an example where the folds themselves are also created using the spatialBlock() function given a specified cv_block_size.

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

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

```
ggplot() +
  geom_sf(data = blocks_scbi, fill = "transparent", linetype = "dashed") +
  geom_sf_text(data = growth_scbi %>% sample_n(1000), aes(label = foldID, col = buffer);
```

2.3 Step 3: Identify all focal and corresponding competitor trees

The next step in our analysis sequence is to identify all focal trees and their corresponding 194 competitor trees. More specifically, it identifies all trees that are not part of the buffer 195 region, have a valid growth measurement, and have at least one neighbor within 7.5 of it. 196 The create_focal_vs_comp() functions performs these tasks and returns a new data frame of type sf. On top of the previous arguments comp_dist defining the competition neigh-198 borhood and id indicating which variable uniquely identifies each tree-stem, this function 199 also requires an sf object representation of the spatial cross-validation blocks/folds. In this 200 example, the blocks were manually encoded in blocks_scbi by specifying it's vertices in Section 2.2⁵. We present the resulting data frame below with the foldID variable omitted 202 ⁵We present an alternative method for defining spatial cross-validation blocks is using the

spatialBlock() function from the blockCV package in the Appendix

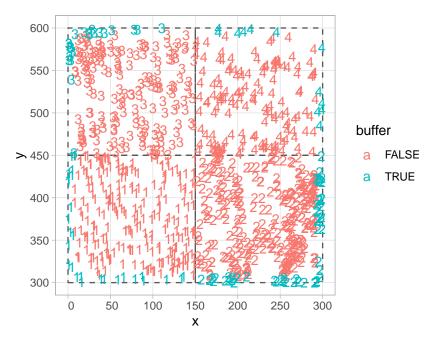


Figure 2: Add spatial information: Buffer region and spatial cross-validation blocks (1 through 4). All trees in the interior of the study region (i.e. not part of buffer) will be the focal trees whose growth will be modeled.

203 for compactness of presentation.

```
focal_vs_comp_scbi <- growth_scbi %>%
  create_focal_vs_comp(comp_dist, blocks = blocks_scbi, id = "stemID")
focal_vs_comp_scbi %>%
  select(-foldID)
## # A tibble: 6,296 x 6
     focal_ID focal_sp
                               geometry growth comp
                         dbh
##
        <dbl> <fct>
                       <dbl>
                                 <POINT> <dbl> <list>
## 1
                       13.6 (14.2 428) 0.103 <tibble [20 x 4]>
            4 nysy
            5 havi
                        8.8
                              (9.4 436) 0.150 <tibble [32 x 4]>
## 2
## 3
           79 tiam
                       47.7
                                (40 381) -0.161 <tibble [20 x 4]>
## 4
                        5.15 (38.7 422) 0.253 <tibble [12 x 4]>
           80 caca
## 5
           96 libe
                        2.3
                                (60 310) 0.262 <tibble [14 x 4]>
```

... with 6,291 more rows

The resulting data frame focal_vs_comp_scbi has 6296 rows, representing the subset of the 7954 trees in growth_scbi that will be considered as focal trees. Two new variables focal_ID and focal_sp relate to tree-stem identification and species information. Most notably however is a new variable comp which contains information on all competitor trees for a given focal tree, saved in tidyr package list-column format (Wickham 2020). For example, we drill-down on the tree with focal_ID 4, which has 20 competitor trees each described by 4 variables as indicated by the fact that comp is a tibble [20 × 4].

The spatial distribution of these trees is visualized in Figure 3: the dashed circle extends
7.5 m away from the focal tree while all 20 competitor trees are within this circle.

Using the unnest() function from the tidyr package, we can flatten list-column into regular columns. We observe that for the same focal tree, we have information on all 20 competitor trees whose dist distance to the focal tree is ≤ 7.5 : their unique tree-stem ID number, their species, and their basal area (in m²) calculated as $\frac{\pi \times (DBH/2)^2}{10000}$ where DBH is the value from the earlier of the two censuses in cm. Saving our focal versus competitor information in list-column minimizes redundancy since we do not repeat information on the focal tree 20 times.

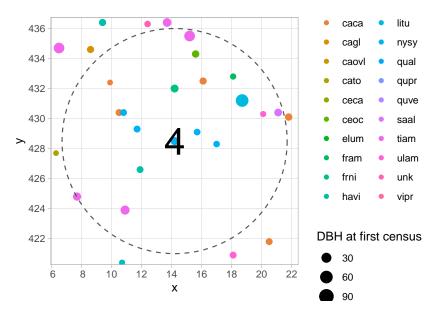


Figure 3: Identify all focal and corresponding competitor trees: All 20 competitor trees of focal tree 4.

```
focal_vs_comp_scbi %>%
  filter(focal_ID == 4) %>%
  select(focal_ID, dbh, comp) %>%
 unnest(cols = "comp")
## # A tibble: 20 x 6
##
     focal_ID
                dbh comp_ID dist comp_sp comp_basal_area
##
        <dbl> <dbl>
                       <dbl> <dbl> <fct>
                                                    <db1>
                            7.48 tiam
## 1
              13.6
                      1836
                                                  0.0176
## 2
              13.6
                     1847 2.81 nysy
                                                  0.00332
## 3
            4 13.6
                      1848 1.62 nysy
                                                  0.00396
## 4
              13.6
                      1849 2.62 nysy
                                                  0.00535
## 5
                            2.98 havi
                                                  0.00472
              13.6
                       1850
## # ... with 15 more rows
```

2.4 Step 4: Fit model

Now that we've identified all focal and corresponding competitor trees and saved this information in a data frame of type focal_vs_comp, the final step in our analysis sequence is to fit a model for the growth of all focal trees. Currently the forestecology package can only fit the competition Bayesian linear regression model outlined in Section ?? using the comp_bayes_lm() function. However, any model implemented in a function that similarly takes an input data frame of type focal_vs_comp as an argument can also be used. For our specific competition Bayesian linear regression model, we also specify prior distributions on all parameters of interest (here chosen to be the defaults as specified in ?comp_bayes_lm).

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

The returned comp_bayes_lm_scbi output is an object of S3 class type comp_bayes_lm
which contains the posterior values of all parameters in our competition Bayesian linear regression. This class of object includes generic methods implemented for print(),
predict(), and ggplot2::autoplot(). First the generic for print() displays the names
of all prior & posterior parameters 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_{-}O
                                      V_star
##
```

```
## Model formula:

## growth ~ sp + dbh + dbh * sp + acne * sp + acpl * sp + acru * sp + acsp * sp + aia
```

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

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

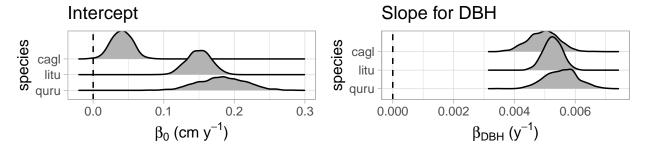
```
focal_vs_comp_scbi
## # A tibble: 6,296 x 8
    focal_ID focal_sp dbh foldID geometry growth
##
       <dbl> <fct> <dbl> <fct>
##
                                    <POINT>
                                           <dbl>
## 1
           4 nysy 13.6 1 (14.2 428) 0.103
## 2
                    8.8 1
                                (9.4 436) 0.150
           5 havi
          79 tiam
                 47.7 1
## 3
                                 (40 381) -0.161
## 4
                    5.15 1
                            (38.7 422) 0.253
          80 caca
                      2.3 1
                                   (60 310) 0.262
## 5
          96 libe
## # ... with 6,291 more rows, and 2 more variables: comp <list>,
      growth_hat <dbl>
```

We then compare the observed and fitted/predicted growths to compute the root mean squared error (RMSE) of our model fit.

```
model_rmse <- focal_vs_comp_scbi %>%

rmse(truth = growth, estimate = growth_hat) %>%

pull(.estimate)
```



Competitor species in rows, focal species in columns Ex: Top row, second column: competitive effect of cagl on litu

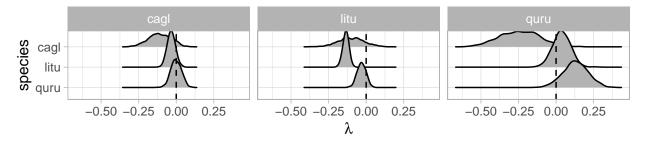


Figure 4: Fit model: Posterior distributions of all parameters for three species.

Lastly, the generic for ggplot2::autoplot() allows us to plot the posterior distribution
of all parameters in Figure 4 (for compactness we only show posteriors for 3 species).

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

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

These plots give the posterior distributions of parameters from Equation 1. For many package users they will be of interest because they give insight into the species-specific competitive interactions. Setting type = "intercepts" gives posterior distributions for $\beta_{0,j}$ and type = "dbh_slopes" for $\beta_{dbh,j}$. These give species specific growth independent of competition. The values of more interest are plotted with type = 'competition' which gives the posterior distribution for $\lambda_{j,k}$ species-specific competition coefficients (i.e., the λ -matrix). Negative values indicate a competitor species which slows the growth of a focal species. Here, for example, we see that tulip trees (litu) have a strong negative effect on the growth of conspecifics but relatively little effect on neighbors of the other two species.

2.5 Evaluate the effect of competitor species identity using permutation tests

In order to evaluate the effect of competitor species identity, we use the four steps of our 253 analysis sequence answer along with a permutation test: Under a null hypothesis where competitor species identity does not matter, we can permute/shuffle this variable within 255 each focal tree, compute the RMSE (the test statistic of interest), repeat this process several times to construct a null distribution of the RMSE, and compare it to the observed RMSE 257 to assess significance. Going back to our example in Section 2.3 of focal tree with focal_ID 4 258 and its 20 competitors, the permutation test randomly resamples the comp_sp variable with 259 replacement, leaving all other variables intact. The resampling with replacement is nested 260 within each focal tree in order to preserve the neighborhood structure of our competition 261 model. To run the permutation test, we use the same comp_bayes_lm() function as in 262 Section 2.4, but with a run_shuffle = TRUE argument.

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

```
focal_vs_comp_scbi <- focal_vs_comp_scbi %>%
  mutate(growth_hat_shuffle = predict(comp_bayes_lm_scbi_shuffle, newdata = focal_vs_com
  model_rmse_shuffle <- focal_vs_comp_scbi %>%
  rmse(truth = growth, estimate = growth_hat_shuffle) %>%
  pull(.estimate)
model_rmse_shuffle
## [1] 0.131
```

The resulting RMSE of 0.131 based on the permutation test is larger than the earlier RMSE of 0.128, suggesting that models that do incorporate competitor species identity better fit the data. We conduct an analysis of the full SCBI plot in Section below.

2.6 Evaluate model performance using spatial cross-validation

We answer the second of our two questions: how can we obtain an accurate estimate of model performance/error? 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.

To this end, we use the foldID variable defined in Section 2.2 whereby all focal trees are assigned to one of 4 spatially contiguous blocks that act as folds in our cross-validation routine. Figure 5 presents a schematic illustrating this scheme for fold 1 (bottom-left) as the test set and folds 2, 3, and 4 as the training sets. We fit the model to all focal trees in the training set, apply the model to all focal trees in the test set to compute fitted/predicted values, and compute the RMSE of the observed versus predicted growths.

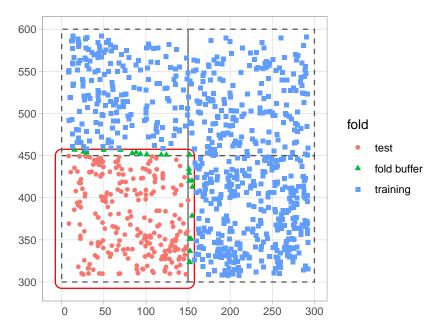


Figure 5: Schematic of spatial cross-validation: Using the k=1 fold as the test set, assigning each focal tree to training set, test set, and fold buffer.

We repeat this procedure 3 more times with each of the three remaining folds acting as
the test set and then average all four resulting RMSE's. Furthermore, in order to maintain
spatial independence between the test and training set, a fold buffer that extend outwards
from the boundary of the test set is computed; all trees falling within this fold buffer are
excluded from the training set.

This algorithm is implemented in the run_cv() function, which is a wrapper function to
the comp_bayes_lm() function that fits the model and the predict() generic that returns
fitted/predicted values. We compare these values to the observed growth values to again
compute our RMSE.

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

```
model_rmse_cv <- focal_vs_comp_scbi %>%

rmse(truth = growth, estimate = growth_hat) %>%

pull(.estimate)
```

model_rmse_cv

[1] 0.14

The resulting RMSE of 0.14 computed using cross-validation is larger than the earlier RMSE of 0.128, suggesting that models that do not take the inherent spatial autocorrelation of the data into account generate error estimates that are overly optimistic; in our case RMSE's that are too low.

3 Discussion

- ²⁹⁵ The forestecology package provides
- Run full simulation on SCBI data
- run time considerations

²⁹⁸ 4 Acknowledgments

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5 Author's contributions

A.Y.K. and D.N.A. conceived the ideas and coded most of the package in the early design stages. A.Y.K. led the writing of the manuscript. S.P.C. refactored much of the package's code in the later design stages to align with R and "tidy" programming best practices (Wickham et al. 2019). All authors contributed critically to the drafts and gave final approval for publication.

308 6 Data accessibility

- We intend to archive all data and code on GitHub at the following repository https://
- 310 github.com/rudeboybert/forestecology. This repository will be versioned and archived
- on Zenodo upon acceptance.

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