The forestecology R package for fitting and assessing neighborhood models of the effect of interspecific competition on the growth of trees

Albert Y. Kim *
Program in Statistical & Data Sciences, Smith College and
David N. Allen
Biology Department, Middlebury College and
Simon P. Couch
Mathematics Department, Reed College

August 10, 2021

Abstract

1. Neighborhood competition models are powerful tools to measure the effect of interspecific competition. Statistical methods to ease the application of these models are currently lacking.

- 2. We present the forestecology package providing methods to i) specify neighborhood competition models, ii) evaluate the effect of competitor species identity using permutation tests, and iii) measure model performance using spatial cross-validation. Following Allen & Kim (2020), we implement a Bayesian linear regression neighborhood 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 research sites. Given ForestGEO's data collection protocols and data formatting standards, the package was designed with cross-site compatibility in mind. We highlight the importance of spatial cross-validation when interpreting model results.
- 4. The package features i) tidyverse-like structure whereby verb-named functions

^{*}Assistant Professor, Statistical & Data Sciences, Smith College, Northampton, MA 01063 (e-mail: akim04@smith.edu).

can be modularly "piped" in sequence, ii) functions with standardized inputs/outputs
of simple features sf package class, and iii) 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 data. Furthermore, while the package only has Bayesian linear regression
implemented, the package was designed with extensibility to other methods in mind.

Keywords: forest ecology, interspecific competition, neighborhood competition, tree growth,
 R, ForestGEO, spatial cross-validation

2

1 Introduction

Repeat-censused forest plots offer excellent opportunities to test neighborhood models of the effect of competition on the growth of trees (Canham et al. 2004). Neighborhood mod-33 els of competition have been used to: test whether the species identity of a competitor 34 matters [Uriarte et al. (2004); measure species-specific competition coefficients (Das 2012, 35 Tatsumi et al. (2016)); test competing models to see what structures competitive interac-36 tions, e.g. traits or phylogeny (Allen & Kim 2020, Uriarte et al. 2010); and inform selective 37 logging practices (Canham et al. 2006). Although these are well-described methods, few 38 methods are currently available for easy application. 39 We address this shortcoming with the forestecology R package providing methods 40 and data for forest ecology model fitting and assessment, available on CRAN (https:// 41 cran.r-project.org/package=forestecology) and on GitHub (https://github.com/ 42 rudeboybert/forestecology). The package is written to model stem diameter growth between two censuses based on neighborhood competition, largely following the methods in Allen & Kim (2020). 45 Let $i = 1, ..., n_j$ index all n_j trees of "focal" species j; let j = 1, ..., J index all J focal 46 species; and let k = 1, ..., K index all K "competitor" species. The average annual growth in diameter at breast height (DBH) y_{ij} (in centimeters/year) of the i^{th} tree of focal species j is modeled as

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

where $\beta_{0,j}$ is the diameter-independent growth rate of species j; dbh_{ij} is the DBH of the focal tree at the earlier census and $\beta_{\text{dbh},j}$ the slope of that species's diameter-growth relationship; x_{ijk}^{comp} is the sum of some numerical explanatory variable of all trees of competitor species k, and λ_{jk} quantifies the corresponding change in growth for individuals of species j from these competitors; and ϵ_{ij} is a random error term distributed Normal $(0, \sigma^2)$. Allen & Kim (2020) use the sum of the basal area of all trees of competitor species k as x_{ijk}^{comp} . Furthermore, they estimate all parameters via Bayesian linear regression, while exploiting Normal/Inverse Gamma conjugacy to derive closed-form solutions to all posterior distributions¹. These closed-form solutions are not as computationally expensive as approximations from Markov Chain Monte Carlo algorithms.

To evaluate whether competitor species identity matters, Allen & Kim (2020) run a permutation test where a null hypothesis of no species grouping-specific effects of competition is assumed, thus the species identity of all competitors can be permuted:

$$H_0: \lambda_{jk} = \lambda_j \text{ for all } k = 1, \dots, K$$
 vs. $H_A:$ at least one λ_{jk} is different

Furthermore, to account for the spatial autocorrelation in their estimates of out-of-63 sample model error, Allen & Kim (2020) use spatial cross-validation. Estimates of model 64 error that do not account for this dependence tend to underestimate the true model error 65 (Roberts et al. 2017). 66 The package is designed with "tidy" design principles in mind (Wickham et al. 2019). 67 Much like all tidyverse packages, forestecology has verb-named functions that can be 68 modularly composed using the pipe %>% operator to sequentially complete all necessary 69 analysis steps (Bache & Wickham 2020). 70 Furthermore, the inputs and outputs of most functions use the same "simple features

Furthermore, the inputs and outputs of most functions use the same "simple features for R" data structures for spatial data from the sf package (Pebesma 2018). Previously sp package classes were commonly used for storing spatial data and interfacing with geospatial libraries (Bivand et al. 2013); the sf package aims to improve on the sp package by:

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

- 1. Using simple feature access as the base standard for representing and encoding spatial data, rather than shapefiles (Herring 2011).
- 2. Leveraging improvements in external libraries for reading and writing spatial data (GDAL) and for geometrical operations (GEOS) (Warmerdam 2008, Team (2017)).
- 3. Integrating closely with the popular tidyverse suite of packages for data science (Wickham et al. 2019).
- By using the sf package classes to represent spatial data rather than the sp package,
- the implementation and use of the forestecology package's spatial algorithms was greatly
- 83 simplified.

$_{84}$ 2 forestecology workflow: a case study

- We present a case-study of forestecology's functionality on data from the Smithsonian
- 86 Conservation Biology Institute (SCBI) large forest dynamics plot in Front Royal, VA,
- 87 USA, part of the ForestGEO global network of research sites (Bourg et al. 2013, Anderson-
- ⁸⁸ Teixeira et al. (2015), Davies et al. (2021)). 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
- ₉₀ Ridge, Ridge and Valley, and Piedmont provinces—and is adjacent to the northern end of
- 91 Shenandoah National Park.
- The package has the following goals: to evaluate i) the effect of competitor species
- 93 identity using permutation tests and ii) model performance using spatial cross-validation.
- We outline the four-step basic analysis sequence:
- 1. Compute the growth of stems based on two censuses.
- 96 2. Add spatial information:

97

98

- 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.

101

103

104

112

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

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

# Resolve conflicting functions
filter <- dplyr::filter
select <- dplyr::select</pre>
```

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

We first compute the growth of trees using data from two censuses. compute_growth()
computes the average annual growth based on census data that roughly follows ForestGEO
standards. Despite such standards, minor variations will still exist between sites, thereby
necessitating some data wrangling. For example, the SCBI site records all DBH values in
millimeters (Bourg et al. 2013), whereas the Michigan Big Woods site used in Allen & Kim
(2020) records them in centimeters (Allen et al. 2020).

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

¹¹³ 2021/08/02 and perform minor data wrangling (Gonzalez-Akre, McGregor, Anderson-¹¹⁴ Teixeira, Dow, Herrmann, Terrell, Kim, Vinod & Helcoski 2020). We then only consider ¹¹⁵ a 9 ha subsection of the 25.6 ha of the site to speed up computation for this example: gx ¹¹⁶ from 0–300 instead of 0–400 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(
    # Convert date from character to date
   date = mdy(date),
    # Convert dbh to be in cm
   dbh = as.numeric(dbh) / 10
 ) %>%
 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))
```

These two data frames are then used as inputs to compute_growth(), along with id specifying the variable that uniquely identifies each tree-stem. We also discard all resprouts with code == R in the later census, since we are only interested in the 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 %>%
    select(stemID, sp, dbh1, dbh2, growth, geometry)
## Simple feature collection with 7954 features and 5 fields
## Geometry type: POINT
## Dimension:
                 XY
## Bounding box: xmin: 0.2 ymin: 300 xmax: 300 ymax: 600
## CRS:
                 NA
## # A tibble: 7,954 x 6
     stemID sp
                  dbh1 dbh2 growth geometry
##
      <\!db\,l> <\!fct> <\!db\,l> <\!db\,l>
                                            <POINT>
         4 nysy 13.6 14.2 0.103 (14.2 428)
## 1
         5 havi 8.8 9.6 0.150 (9.4 436)
## 2
## 3
        6 havi 3.25 4 0.140 (1.3 434)
        77 qual 65.2 66 0.141 (34.7 307)
## 4
        79 tiam 47.7 46.8 -0.161 (40 381)
## 5
## # ... with 7,949 more rows
```

The output growth_scbi is a data frame of class sf that includes among other variables
the species variable sp converted to a factor, the average annual growth in DBH (cm ·
y-1) for all stems that were alive at both time points, and the sf package's encoding of
geolocations of geometry type <POINT>. Given that growth_scbi is of class sf, it can be
easily plotted in ggplot2 using geom_sf() as seen in Figure 1.

```
ggplot() + geom_sf(data = growth_scbi %>%
    sample_n(500), aes(size = growth)) + scale_size_binned(limits = c(0.1,
    1)) + labs(size = expression(paste(Growth, " (cm ", y^{{
```

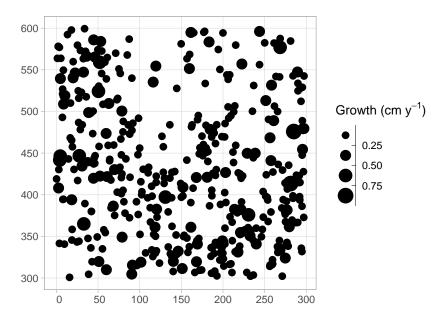


Figure 1: Step 1 - Compute growth of trees based on census data. A map of the growth of a random sample of 500 trees from a 9 ha subsection of the Smithsonian Conservation Biology Institute (SCBI) forest plot.

```
-1
}, ")")))
```

We also load species information as it existed on GitHub on 2021/08/02, which includes family, genus, and species information; as well as classifications of the canopy position (canopy, canopy emergent, understory, shrub layer), drought tolerance (intolerant,
resistant), and other characteristics of the species.

```
sp_info <- read_csv("SCBI_ForestGEO_sp_ecology.csv") %>%
    select(sp = spcode, family, genus, species, canopy_position, drought_tolerance)
sp_info
## # A tibble: 65 x 6
##
                                                     canopy\_position\ drought\_toleran~
            family
                                        species
                           genus
     < chr > < chr >
                             < chr>
                                           < chr >
                                                         < chr >
                                                                           < chr >
## 1 acne Sapindaceae
                                                                      drought-resista~
                           Acer
                                        nequndo
                                                     understory
```

```
## 2 acpl Sapindaceae
                         Acer
                                     platanoides canopy
                                                                  drought-resista~
## 3 acru Sapindaceae
                         Acer
                                                                  drought-resista~
                                     rubrum
                                                  canopy
## 4 aial Simaroubaceae Ailanthus
                                                                  drought-resista~
                                     altissima
                                                  canopy
                         Amelanchier arborea
## 5 amar Rosaceae
                                                  understory
                                                                  drought-resista~
## # ... with 60 more rows
```

We join this species information to our growth_scbi data frame and convert the species variable to a factor.

```
growth_scbi <- growth_scbi %>%

left_join(sp_info, by = "sp") %>%

mutate(sp = as.factor(sp))
```

Furthermore, we compute two potential competitor explanatory variables x_{ijk}^{comp} from Equation 1. First, the basal area of each tree as a function of its DBH in the earlier census. Second, the above ground biomass as estimated by allometric equations encoded in the get_biomass() function from the allodb package (Gonzalez-Akre, Piponiot, Lepore & Anderson-Teixeira 2020); this function has DBH, species, and geographic coordinates as arguments.

```
# Install development version of allodb using:
# remotes::install_github("forestgeo/allodb")
library(allodb)
growth_scbi <- growth_scbi %>%
mutate(
    # Compute basal area:
basal_area = 0.0001 * pi * (dbh1 / 2)^2,
# Compute above ground biomass:
agb = get_biomass(
```

```
dbh = dbh1,
    genus = genus,
    species = species,
    coords = c(-78.2, 38.9)
)
```

¹³⁸ 2.2 Step 2: Add spatial information

We then add spatial information to growth_scbi. We first add a "buffer region" to the periphery of the study region. Since some of our model's explanatory variables are cumulative, 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 the study region who will not have all their neighbors included in the census stems. 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 competitor 146 trees are: all trees within a distance comp_dist of a focal tree. Here we set comp_dist to 147 7.5m, a value informed by other studies (Canham et al. 2004, Uriarte et al. (2004), Canham 148 et al. (2006)), but the package could also be used to compare multiple distances and see 149 which is best supported (see Appendix A). We use comp_dist and a manually constructed 150 sf representation of the study region's boundary as inputs to add_buffer_variable() to 151 add a buffer boolean variable to growth_scbi. All trees with buffer equal to FALSE will 152 be our focal trees whose growth will be modeled, whereas those with TRUE will only act as 153 competitor trees. 154

```
# Define competitive distance range
comp_dist <- 7.5

# Manually construct study region boundary
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 we add are blocks corresponding to folds 155 of a spatial cross-validation algorithm. Conventional cross-validation algorithms assign 156 individual observations to folds by randomly resampling them all while assuming they are 157 statistically independent. In the case of forest census data however, observations exhibit 158 spatial autocorrelation. We therefore incorporate this dependence into the cross-validation 159 algorithm by resampling spatial blocks of trees (Roberts et al. 2017, Pohjankukka et al. 160 (2017)). 161 We first manually define an sf object defining four folds that partition the study region. 162 We then use the output of the spatialBlock() function from the blockCV package to 163 associate each tree in growth_scbi to the correct foldID (Valavi et al. 2019). This foldID 164 variable will be used in Section 2.6. 165 Figure 2 illustrates the net effect of adding these two elements of spatial information to 166 growth_scbi. 167

```
# Manually define spatial blocks to act as folds
n_fold <- 4
fold1 <- cbind(c(0, 150, 150, 0), c(300, 300, 450, 450))</pre>
```

```
fold2 \leftarrow cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))
fold3 <- cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))
fold4 \leftarrow cbind(c(150, 300, 300, 150), c(450, 450, 600, 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,</pre>
    selection = "systematic", blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE)
growth_scbi <- growth_scbi %>%
    mutate(foldID = spatial_block_scbi$foldID %>%
        factor())
ggplot() + geom_sf(data = blocks_scbi, fill = "transparent", linetype = "dashed") +
    geom_sf_text(data = growth_scbi %>%
        sample_n(1000), aes(label = foldID, col = buffer))
```

⁶⁸ 2.3 Step 3: Identify all focal and corresponding competitor trees

We then identify all focal trees and their corresponding competitor trees. More specifically, identify all trees that are not part of the buffer region, have a valid growth measurement, and have at least one neighbor within 7.5m. We do this using create_focal_vs_comp(), which takes the previously detailed comp_dist and id arguments, the sf representation

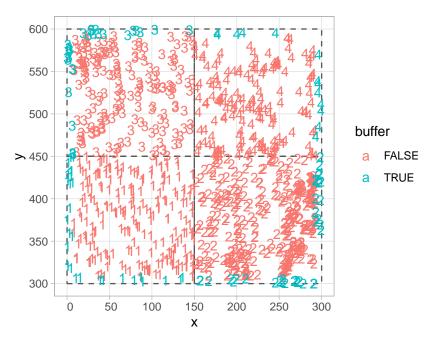


Figure 2: Step 2 - Add spatial information. A buffer region and spatial cross-validation blocks 1 through 4. The location of each tree is marked with its fold number where the folds are delineated with solid lines. The color of each digit indicates whether the tree is part of the buffer region (thus will only be considered as a competitor tree) or is part of the interior of the study region (thus is a focal tree whose growth is of modeled interest).

of the spatial cross-validation blocks blocks_scbi, and a specification comp_x_var of the basal_area variable we use as the competitor explanatory variable x_{ijk}^{comp} from Equation 1.

This function returns a new data frame focal_vs_comp_scbi.

183

The resulting focal_vs_comp_scbi has 6296 rows, representing the subset of the 7954 trees in growth_scbi that will be considered as focal trees. The variables focal_ID and focal_sp relate to tree-stem identification and species information. Most notably however is the variable comp, which contains information on all competitor trees saved in tidyr package list-column format (Wickham 2020). To inspect this information, we flatten the comp list-column for the tree with focal_ID 4 in the first row, here a tibble [20 × 4], into regular columns using unnest() from the tidyr package.

```
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_x_var
         < db \, l > < db \, l >
                           < db \, l > < db \, l > < fc \, t >
##
                                                           < db \, l >
## 1
                 13.6
                          1836
                                 7.48 tiam
                                                   0.0176
                 13.6
                          1847 2.81 nysy
## 2
                                                   0.00332
                 13.6
## 3
                          1848 1.62 nysy
                                                   0.00396
## 4
                 13.6
                          1849
                                2.62 nysy
                                                   0.00535
## 5
                 13.6
                          1850
                                2.98 havi
                                                   0.00472
## # ... with 15 more rows
```

We observe 4 variables describing 20 competitor trees: the unique tree-stem ID, the

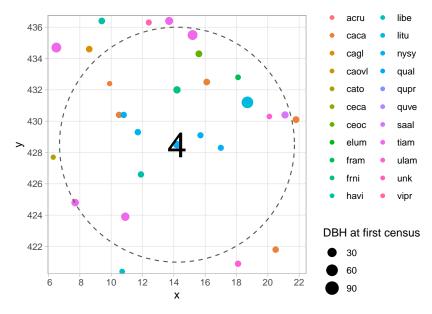


Figure 3: Step 3 - Identify all focal and corresponding competitor trees. The dashed circle extends 7.5m away from the focal tree 4 while all 20 competitor trees are within this circle.

distance to the focal tree (all \leq 7.5m), the species, and the basal area (in m²) calculated as $\frac{\pi \times (DBH/2)^2}{10000}$ for the DBH in cm from the earlier census. Saving competitor information in list-column format minimizes redundancy since we do not need to repeat information on the focal tree 20 times. We visualize the spatial distribution of these trees in Figure 3.

Here we use basal area as the continuous competitor explanatory variable but the pack-188 age is flexible to allow the user to specify any competitor explanatory variable (basal area, 189 biomass, tree height, a soil nutrient value, ...). The package can also be used to compare 190 competitor explanatory variables and see which best explains tree growth, see Appendix 191 B for an example comparing basal area and above ground biomass. Similarly, the package 192 can use any categorical variable as an explanatory variable and compare between different 193 categorical variables. For example in Allen & Kim (2020) we compare grouping individ-194 uals based on species, family, and based on trait-based groups. In Appendix C we give 195 another example and compare grouping individuals by species or by potential canopy po-196 sition (canopy, understory, shrub layer). 197

198 2.4 Step 4: Fit model

Lastly, we fit the competition Bayesian linear regression model for tree growth outlined in Equation 1 using comp_bayes_lm(). This function has an option to specify prior distributions of all parameters, chosen here to be the defaults detailed in ?comp_bayes_lm.

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

The resulting comp_bayes_lm_scbi is an object of S3 class type comp_bayes_lm containing the posterior values of all parameters. Furthermore, this class includes generics for three methods. First, the generic for print() displays the names of all prior and posterior parameters and the model formula:

```
comp_bayes_lm_scbi
## Bayesian linear regression model parameters with a multivariate Normal
## likelihood. See ?comp_bayes_lm for details:
##
     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
                                     \mathit{mu\_star}
## 4 Multivariate t on beta
                               V_{-}O
                                     V_star
##
## Model formula:
## growth \sim sp + dbh + dbh * sp + acne * sp + acru * sp + amar * sp + astr
## * sp + caca * sp + caco * sp + cade * sp + caql * sp + caovl * sp + cato
## * sp + ceca * sp + ceoc * sp + chvi * sp + cofl * sp + crpr * sp + crsp
## * sp + divi * sp + elum * sp + faqr * sp + fram * sp + frni * sp + frpe
```

```
## * sp + havi * sp + ilve * sp + juci * sp + juni * sp + libe * sp + litu
## * sp + nysy * sp + pist * sp + pivi * sp + ploc * sp + prav * sp + prse
## * sp + qual * sp + quco * sp + qufa * sp + qumi * sp + qupr * sp + quru
## * sp + quve * sp + rops * sp + saal * sp + saca * sp + tiam * sp + ulam
## * sp + ulru * sp + unk * sp + vipr * sp
```

Next, the generic for predict() takes the posterior parameter values in comp_bayes_lm_scbi and a newdata data frame, and outputs a vector growth_hat of predicted DBH values $\widehat{y_{ij}}$ 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 %>%
    select(focal_ID, focal_sp, dbh, growth, growth_hat)
## # A tibble: 6,296 x 5
     focal_ID focal_sp    dbh growth growth_hat
##
        < db \, l > < fc \, t >  < db \, l > 
                                              < db \, l >
## 1
                       13.6
                              0.103
                                         0.0809
            4 nysy
## 2
            5 havi
                       8.8
                              0.150
                                         0.112
## 3
           79 tiam
                       47.7 -0.161
                                         0.229
## 4
           80 caca
                     5.15 0.253
                                         0.121
## 5
           96 libe
                        2.3
                               0.262
                                         0.142
## # ... with 6,291 more rows
```

We can now compare the observed and predicted growths to compute the root mean squared error (RMSE) of our model:

```
model_rmse <- focal_vs_comp_scbi %>%
    rmse(truth = growth, estimate = growth_hat) %>%
    pull(.estimate)
model_rmse
## [1] 0.128
```

Lastly, the generic for ggplot2::autoplot() allows us to visualize all posterior distributions, as seen in Figure 4. Setting type to "intercepts" and "dbh_slopes" returns species-specific posterior distributions for $\beta_{0,j}$ and $\beta_{dbh,j}$ respectively, while setting type = "competition" returns competition coefficients $\lambda_{j,k}$.

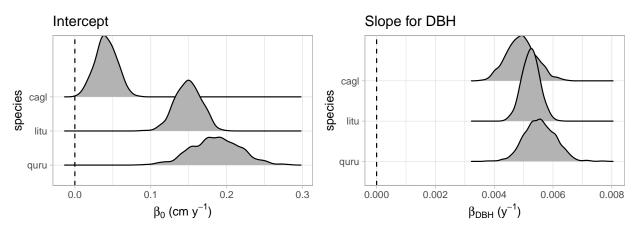
```
# Plot posteriors for only a subset of species
sp_to_plot <- c("litu", "quru", "cagl")

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 the patchwork package
(plot1 | plot2)/plot3</pre>
```

For many users the visualizations of $\lambda_{j,k}$ will be of particular interest as they provide insight into species-specific competitive interactions, where negative values indicate a competitor species which slows the growth of a focal species. Here, for example, we see that tulip poplars (litu) have a strong negative effect on the growth of conspecifics but relatively lesser effect on pignut hickory (cagl) and red oak (quru) neighbors.

Currently the forestecology package can only fit the competition Bayesian linear regression model in Equation 1. However, it can be extended to any model as long as it is



Competitor species in rows, focal species in columns

Ex: Top row, second column: competitive effect of cagl on litu

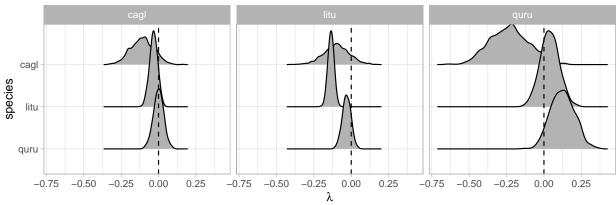


Figure 4: Step 4 - Fit model. Posterior distributions of all parameters. For compactness we include only three species.

235

implemented in a function similar to comp_bayes_lm().

223 2.5 Evaluate the effect of competitor species identity using per224 mutation tests

To evaluate the effect of competitor species identity, we use the above four steps along with 225 the permutation test in Equation 2. Under a null hypothesis where competitor species 226 identity does not matter, we can permute the competitor species identities within each 227 focal tree, compute the RMSE test statistic, repeat this process several times to construct 228 a null distribution, and compare it to the observed RMSE to assess significance. Going 229 back to our example in Section 2.3 of focal tree with focal_ID 4 and its 20 competitors, 230 the permutation test only randomly resamples the comp_sp variable without replacement, 231 leaving all other variables intact. This resampling is nested within each focal tree in order 232 to preserve neighborhood structure. We perform this permutation test once again using 233 comp_bayes_lm() but by setting run_shuffle = TRUE.

```
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_comp_scbi_shuffle)
```

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

The resulting permutation test RMSE of 0.131 is larger than the earlier RMSE of 0.128,

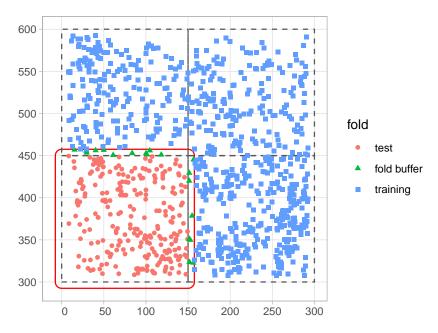


Figure 5: Schematic of spatial cross-validation. Using the k=1 fold (bottom-left) as the test set, k=2 through 4 as the training set, along with a "fold buffer" extending outwards from the test set to maintain spatial independence between it and the training set.

suggesting that models that do incorporate competitor species identity better fit the data.

2.6 Evaluate model performance using spatial cross-validation

To evaluate model performance, we use spatial cross-validation. The model fit in Section 2.4 uses the same data to both fit and assess model performance. Given the spatial-autocorrelation of our data, this can potentially lead to overfit models (Roberts et al. 2017). To mitigate this risk, we use the spatial cross-validation blocking scheme encoded in the foldID variable from Section 2.2 and visualized in Figure 2.

At each iteration of the cross-validation, one fold acts as the test set and the remaining
three act as the training set. We fit the model to all focal trees in the training set, apply
the model to all focal trees in the test set, compute predicted values, and compute the
RMSE. Furthermore, to maintain spatial independence between the test and training sets,
a "fold buffer" that extends 7.5m outwards from the boundary of the test set is considered;
all trees within this "fold buffer" are excluded from the training set (see Figure 5).

257

This process is repeated for each of the four folds acting as the test set, then the four RMSE's are averaged to provide a single estimate of model error. This algorithm is implemented in run_cv(), which acts as a wrapper function to both comp_bayes_lm() that fits the model and predict() that returns predicted values.

```
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 account for spatial autocorrelation generate model error estimates that are overly optimistic, i.e. RMSE values that are too low.

3 Importance of spatial cross-validation

run_cv() also accepts the run_shuffle argument in order to permute competitor species
identity as described in Section 2.5. Figure 6 compares model performance for 49 permutations of competitor species and RMSE calculations, both with and without cross-validation.
Without cross-validation, competitor species identity does matter as the observed RMSE
was significantly lower than the permutation null distribution of RMSE. However, once we
incorporate spatial cross-validation, this improvement disappears. These results suggest
that in this 9 ha subplot of the SCBI plot, competitive interactions do not depend on the

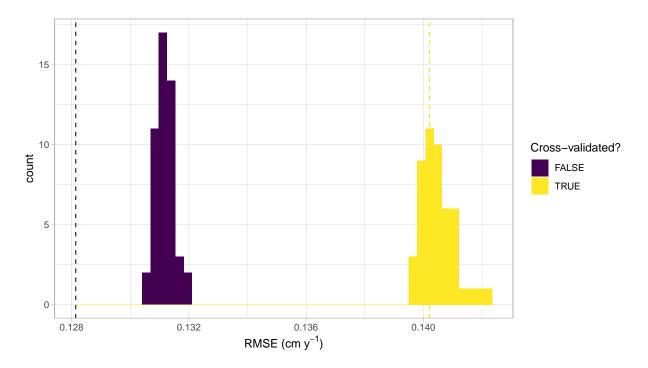


Figure 6: Comparison of root mean squared error of models for standard, permuted, and spatially cross-validated error estimates. The dotted lines show observed RMSE while the histograms show the null distribution of RMSE for 49 permutations under the null hypothesis of no competitor species identity effects. The colors indicate whether spatial cross-validation was used or not.

identity of the competitor, which is the opposite of what has been observed in other locations (Allen & Kim 2020, Uriarte et al. (2004)). This provides a striking example of the importance of cross-validation, as without it the over-fit model gives rise to an incorrect conclusion.

₆₉ 4 Conclusion and future work

The forestecology package provides an accessible way to fit and test models of neighborhood competition. The package follows the tidy data design principles, leverages the sf
package for spatial data, and S3 open-oriented model implementation structure (Pebesma
273 2018). We hope that the package will increase the use of neighborhood competition models
to better understand what structures plant competition.

While the package is designed with ForestGEO plot data in mind, we envision that it can be modified to work on any single large, mapped forest plot in which at least two measurements of each individual have been taken. Furthermore, we hope that future versions of the package will be flexible to other plot layouts, for example inventory plot-structure with many spatially separated plots like the US Forest Service Forest Inventory and Analysis plots (Smith 2002).

We also hope to extend the forestecology package's functionality to account for a larger variety of models for tree growth. One clear future direction would be to allow competition based on species trait values rather than species identity. There is evidence that traits predict competitive outcomes (Kunstler et al. 2012, Lasky et al. (2014), Uriarte et al. (2010)). Thus an extension of the model would allow λ values from Equation 1 to be a function of the traits of competing species.

Lastly, the forestecology current uses the blockCV package behind the scenes to create the spatial blocks acting as folds for our spatial cross-validation algorithm detailed
in Sections 2.2 and 2.6 (Valavi et al. 2019). This back-end functionality could be substituted with the spatialsample package for spatial resampling infrastructure; a tidymodels
package under active development as of 2021 (Silge 2021, Kuhn & Wickham (2020)).

Lastly, currently the package only implements the Bayesian linear regression model detailed in Equation 1. As we demonstrate in Section 2.4 however, the fitting of this model is self-contained in a single function comp_bayes_lm() which returns an object of S3 class type comp_bayes_lm. This class has generic methods implemented to print, make predictions, and plot all results. Therefore the package can be modularly extended to fit other models as long as they are coded similarly to comp_bayes_lm() and have equivalent generic methods implemented.

5 Acknowledgments

We thank Sophie Li for their feedback on the package interface. The authors declare no conflicts of interest.

6 Author's contributions

AYK and DNA conceived the ideas and coded a draft of the package. AYK wrote an initial manuscript draft. SPC rewrote much of the package's code to align with R and "tidy" best practices (Wickham et al. 2019). All authors contributed to subsequent drafts and gave final approval for manuscript.

7 Data accessibility

We intend to archive all data and source code for this manuscript on GitHub at https://
github.com/rudeboybert/forestecology and on Zenodo upon acceptance. The example
Smithsonian Conservation Biology Institute census and species information data are available on GitHub at https://github.com/SCBI-ForestGEO/SCBI-ForestGEO-Data/tree/
master/ and are archived on Zenodo at https://doi.org/10.5281/zenodo.2649301 (GonzalezAkre, McGregor, Anderson-Teixeira, Dow, Herrmann, Terrell, Kim, Vinod & Helcoski
2020).

A Appendix: Compare different competitive distances

For all the above analyses we set the cut off distance (comp_dist) for two stems to compete as 7.5m. This distance has been estimated in previous neighborhood competition studies in forests (Canham et al. 2004, Uriarte et al. (2004), Canham et al. (2006)). We used 7.5m in Allen & Kim (2020) as an average of the values estimated in other studies. But our

package can be used to find which distance is best supported by the data. Here we provide an example using another section of the SCBI plot to provide an additional example of the cross-validation block layout. To speed computation we do not consider species differences in competitive effects and treat all species as the same.

We observe in Figure 7 that a cut-off distance of approximately 6m minimizes the cross-validation estimated RMSE.

```
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
 ) %>%
 filter(gx < 400, gy < 400)
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 < 400, gy < 400)
growth_scbi <-
  compute_growth(
    census_1 = census_2013_scbi,
    census_2 = census_2018_scbi %>% filter(!str_detect(codes, "R")),
```

```
id = "stemID"
  ) %>%
  # make all species the same, needs to be factor with at least two levels
  mutate(sp = factor("A", levels = c("A", "B"))) %>%
  # Compute basal area:
  mutate(basal\_area = 0.0001 * pi * (dbh1 / 2)^2)
study_region_scbi <- tibble(</pre>
 x = c(0, 400, 400, 0, 0),
 y = c(0, 0, 400, 400, 0)
) %>%
  sf_polygon()
n_{-}fold < -4
fold1 <- cbind(c(0, 200, 200, 0), c(0, 0, 200, 200))
fold2 \leftarrow cbind(c(200, 400, 400, 200), c(0, 0, 200, 200))
fold3 <- cbind(c(0, 200, 200, 0), c(200, 200, 400, 400))
fold4 \leftarrow cbind(c(200, 400, 400, 200), c(200, 200, 400, 400))
blocks_scbi <- bind_rows(</pre>
  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 <-</pre>
  spatialBlock(
    speciesData = growth_scbi, k = n_fold,
    selection = "systematic", blocks = blocks_scbi,
    showBlocks = FALSE, verbose = FALSE
  )
growth_scbi <- growth_scbi %>%
  mutate(foldID = spatial_block_scbi$foldID %>% factor())
mult_dist_comp <- tibble(</pre>
  dist = c(5, 6.25, 7.5, 8.75, 10),
 rmse = 0
)
for (i in 1:length(mult_dist_comp$dist)) {
  comp_dist <- mult_dist_comp$dist[i]</pre>
  growth_scbi <- growth_scbi %>%
    add_buffer_variable(size = comp_dist, region = study_region_scbi)
  focal_vs_comp_scbi <- growth_scbi %>%
    create_focal_vs_comp(comp_dist = comp_dist, blocks = blocks_scbi, id = "stemID", comp
    run_cv(comp_dist = comp_dist, blocks = blocks_scbi)
  mult_dist_comp$rmse[i] <- focal_vs_comp_scbi %>%
```

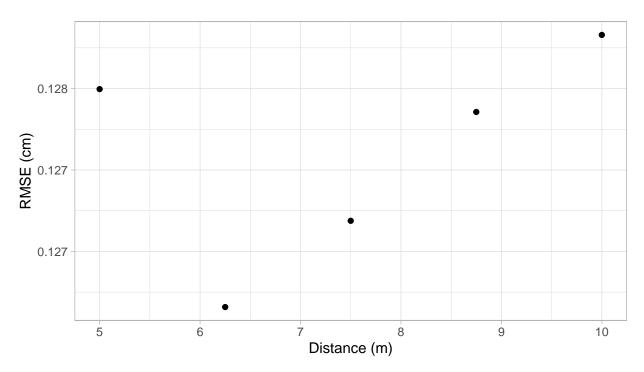


Figure 7: Cross-validated RMSE estimates for 5 competitive distances2.

```
rmse(truth = growth, estimate = growth_hat) %>%
pull(.estimate)
}
```

B Appendix: Compare competitor explanatory variables ables

In the above code we use the basal area of an individual as a continuous competitor explanatory variable. But the package allows the user to specify any competitor explanatory
variable in the comp_x_var argument of create_focal_vs_comp function. Here we use the
cross-validated model comparison to see which of two possible competitor explanatory variables computed in Section 2.1, basal area or above ground biomass, best explains growth.

```
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) %>%
    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))
growth_scbi <- compute_growth(census_1 = census_2013_scbi, census_2 = census_2018_scbi %>
    filter(!str_detect(codes, "R")), id = "stemID") %>%
    left_join(sp_info, by = "sp") %>%
    mutate(sp = as.factor(sp), basal_area = 1e-04 * pi * (dbh1/2)^2, agb = get_biomass(d
        genus = genus, species = species, coords = c(-78.2, 38.9)))
study_region_scbi <- tibble(x = c(0, 300, 300, 0, 0), y = c(300, 300, 600,
    600, 300)) %>%
    sf_polygon()
n\_fold < \texttt{-} \ 4
fold1 \leftarrow cbind(c(0, 150, 150, 0), c(300, 300, 450, 450))
fold2 \leftarrow cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))
fold3 \leftarrow cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))
fold4 \leftarrow cbind(c(150, 300, 300, 150), c(450, 450, 600, 600))
```

```
blocks_scbi <- bind_rows(sf_polygon(fold1), sf_polygon(fold2), sf_polygon(fold3),</pre>
    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,</pre>
    selection = "systematic", blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE)
growth_scbi <- growth_scbi %>%
    mutate(foldID = spatial_block_scbi$foldID %>%
        factor())
comp_dist < -7.5
growth_scbi <- growth_scbi %>%
    add_buffer_variable(size = comp_dist, region = study_region_scbi)
focal_vs_comp_ba <- growth_scbi %>%
    create_focal_vs_comp(comp_dist = comp_dist, blocks = blocks_scbi, id = "stemID",
        comp_x_var = "basal_area") %>%
    run_cv(comp_dist = comp_dist, blocks = blocks_scbi)
focal_vs_comp_agb <- growth_scbi %>%
    create_focal_vs_comp(comp_dist = comp_dist, blocks = blocks_scbi, id = "stemID",
        comp_x_var = "agb") %>%
```

```
run_cv(comp_dist = comp_dist, blocks = blocks_scbi)

focal_vs_comp_ba %>%
    rmse(truth = growth, estimate = growth_hat) %>%
    pull(.estimate)

## [1] 0.14

focal_vs_comp_agb %>%
    rmse(truth = growth, estimate = growth_hat) %>%
    pull(.estimate)

## [1] 2.08
```

Here we observe that basal area is a better competitor explanatory variable competitor explanatory variables x_{ijk}^{comp} from Equation 1 than above ground biomass as suggested by the lower estimated RMSE.

336 C Appendix: Compare grouping variables

- The package also allows the user to specify the categorical explanatory grouping variable.
- Here we compare two different such variables: species and the potential canopy position of
- that species. If we had individual-level crown classes (Smith (1986) dominant, codominant,
- intermediate and suppressed) that could also be used.

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

```
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))
growth_scbi_sp <- compute_growth(census_1 = census_2013_scbi, census_2 = census_2018_scbi</pre>
    filter(!str_detect(codes, "R")), id = "stemID") %>%
    mutate(sp = as.factor(sp), basal_area = 1e-04 * pi * (dbh1/2)^2)
growth_scbi_can_pos <- compute_growth(census_1 = census_2013_scbi, census_2 = census_2018_
    filter(!str_detect(codes, "R")), id = "stemID") %>%
    left_join(sp_info, by = "sp") %>%
    mutate(canopy_position = str_replace(canopy_position, " ", "_"), canopy_position = st
        ",", ""), canopy_position = ifelse(is.na(canopy_position), "shrub_layer",
        canopy_position), sp = as.factor(canopy_position), basal_area = 1e-04 *
        pi * (dbh1/2)^2
study_region_scbi <- tibble(x = c(0, 300, 300, 0, 0), y = c(300, 300, 600,
    600, 300)) %>%
    sf_polygon()
n_{-}fold < -4
fold1 \leftarrow cbind(c(0, 150, 150, 0), c(300, 300, 450, 450))
fold2 \leftarrow cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))
fold3 <- cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))
fold4 \leftarrow cbind(c(150, 300, 300, 150), c(450, 450, 600, 600))
```

```
blocks_scbi <- bind_rows(sf_polygon(fold1), sf_polygon(fold2), sf_polygon(fold3),</pre>
    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,</pre>
    selection = "systematic", blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE)
growth_scbi_sp <- growth_scbi_sp %>%
    mutate(foldID = spatial_block_scbi$foldID %>%
        factor())
growth_scbi_can_pos <- growth_scbi_can_pos %>%
    mutate(foldID = spatial_block_scbi$foldID %>%
        factor())
comp_dist < -7.5
growth_scbi_sp <- growth_scbi_sp %>%
    add_buffer_variable(size = comp_dist, region = study_region_scbi)
growth_scbi_can_pos <- growth_scbi_can_pos %>%
    add_buffer_variable(size = comp_dist, region = study_region_scbi)
focal_vs_comp_sp <- growth_scbi_sp %>%
    create_focal_vs_comp(comp_dist = comp_dist, blocks = blocks_scbi, id = "stemID",
        comp_x_var = "basal_area") %>%
```

We find that species identity has a lower RMSE, so does a better job. We still however plot the competition posteriors for the canopy position groupings in Figure 8. Unsurprisingly we see that canopy and canopy emergent competitors generally have negative effects on their neighbors, while shrubs and understory competitors have neutral or even positive effects.

```
fit_mod_can_pos <- growth_scbi_can_pos %>%
    create_focal_vs_comp(
    comp_dist = comp_dist,
    blocks = blocks_scbi,
    id = "stemID",
```

Competitor species in rows, focal species in columns

Ex: Top row, second column: competitive effect of canopy on canopy_emerg

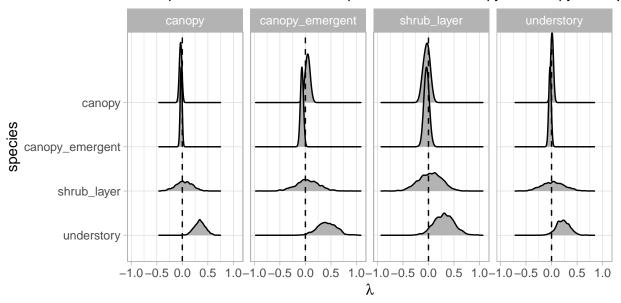


Figure 8: Posterior distributions of all competition parameters.

```
comp_x_var = "basal_area"
) %>%
comp_bayes_lm(prior_param = NULL)
```

D Appendix: Replicate RMSE comparison

This code replicates Figure 6: A comparison of root mean squared error of models for standard, permuted, and spatial cross-validated error estimates.

```
library(tidyverse)
library(lubridate)
library(here)
library(sf)
library(viridis)
```

```
library(forestecology)
library(blockCV)
library(tictoc)
# Compute growth of trees based on census data
census_2013_scbi <- here("paper/scbi.stem2.csv") %>%
   read_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))
census_2018_scbi <- here("paper/scbi.stem3.csv") %>%
   read_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))
growth_scbi <- compute_growth(census_1 = census_2013_scbi, census_2 = census_2018_scbi %>
    filter(!str_detect(codes, "R")), id = "stemID") %>%
    # Compute basal area:
mutate(basal\_area = 1e-04 * pi * (dbh1/2)^2)
# Add spatial information
```

```
# ----- 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)
# Manually define spatial blocks to act as folds
fold1 <- rbind(c(0, 300), c(150, 300), c(150, 450), c(0, 450))
fold2 \leftarrow 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 \leftarrow rbind(c(150, 450), c(300, 450), c(300, 600), c(150, 600))
n_{fold} < -4
blocks_scbi <- bind_rows(sf_polygon(fold1), sf_polygon(fold2), sf_polygon(fold3),</pre>
    sf_polygon(fold4)) %>%
   mutate(folds = c(1:n_fold) %>%
        factor())
# Associate each observation to a fold
SpatialBlock_scbi <- spatialBlock(speciesData = growth_scbi, k = n_fold,</pre>
    selection = "systematic", blocks = blocks_scbi, showBlocks = FALSE, verbose = FALSE)
```

```
growth_scbi <- growth_scbi %>%
   mutate(foldID = SpatialBlock_scbi$foldID %>%
       factor())
# Compute focal versus competitor tree information
# -----
focal_vs_comp_scbi <- growth_scbi %>%
   create_focal_vs_comp(comp_dist, blocks = blocks_scbi, id = "stemID",
       comp_x_var = "basal_area")
# Fit model and make predictions
# ----- Number of permutation
# shuffles:
num\_shuffle <- 49
# Save results here
run_time <- 0
observed_RMSE <- 0
observed_RMSE_CV <- 0
shuffle_RMSE <- vector("list", 1)</pre>
shuffle_RMSE_CV <- vector("list", 1)</pre>
filename <- here("paper/simulation_results/") %>%
   str_c("2021-03-03_scbi_", num_shuffle, "_shuffles")
# Run all simulations O. Setup simulation for this species type ----
```

```
# Start clock
tic()
# 1. Compute observed test statistic: RMSE with no cross-validation
# ---- Fit model (compute posterior parameters)
comp_bayes_lm_scbi <- focal_vs_comp_scbi %>%
    comp_bayes_lm(prior_param = NULL, run_shuffle = FALSE)
# Make predictions and compute RMSE
observed_RMSE <- focal_vs_comp_scbi %>%
   mutate(growth_hat = predict(comp_bayes_lm_scbi, focal_vs_comp_scbi)) %>%
    rmse(truth = growth, estimate = growth_hat) %>%
   pull(.estimate)
# 2. Compute observed test statistic: RMSE with cross-validation
# -----
observed_RMSE_CV <- focal_vs_comp_scbi %>%
   run_cv(comp_dist = comp_dist, blocks = blocks_scbi) %>%
    rmse(truth = growth, estimate = growth_hat) %>%
   pull(.estimate)
# 3. Permutation distribution: RMSE with no cross-validation
# ----- Compute num_shuffle permutation test statistics
shuffle_RMSE <- numeric(length = num_shuffle)</pre>
for (j in 1:num_shuffle) {
    # Fit model (compute posterior parameters) with shuffling
```

```
comp_bayes_lm_scbi <- focal_vs_comp_scbi %>%
        comp_bayes_lm(prior_param = NULL, run_shuffle = TRUE)
    # Make predictions and compute RMSE
    shuffle_RMSE[j] <- focal_vs_comp_scbi %>%
       mutate(growth_hat = predict(comp_bayes_lm_scbi, focal_vs_comp_scbi)) %>%
        rmse(truth = growth, estimate = growth_hat) %>%
       pull(.estimate)
}
# 4. Permutation distribution: RMSE with cross-validation
# ----- Compute num_shuffle permutation test statistics
shuffle_RMSE_CV <- numeric(length = num_shuffle)</pre>
# Compute num_shuffle permutation test statistics
for (j in 1:num_shuffle) {
    # Compute and save RMSE
    shuffle_RMSE_CV[j] <- focal_vs_comp_scbi %>%
        run_cv(comp_dist = comp_dist, blocks = blocks_scbi, run_shuffle = TRUE) %>%
        rmse(truth = growth, estimate = growth_hat) %>%
       pull(.estimate)
    # Status update
    str_c("Shuffle with permutation ", j, " at ", Sys.time()) %>%
       print()
```

```
# 5. Save results ----
clock <- toc(quiet = TRUE)</pre>
run_time <- clock$toc - clock$tic</pre>
model_comp_tbl <- tibble(run_time = run_time, observed_RMSE = observed_RMSE,</pre>
    observed_RMSE_CV = observed_RMSE_CV, shuffle_RMSE = shuffle_RMSE, shuffle_RMSE_CV = sh
    )
save(model_comp_tbl, file = filename %>%
   str_c(".RData"))
# Visualize results
                 _____
model_comp <- bind_rows(model_comp_tbl %>%
    select(run_time, observed = observed_RMSE, shuffle = shuffle_RMSE) %>%
   mutate(CV = FALSE), model_comp_tbl %>%
    select(run_time, observed = observed_RMSE_CV, shuffle = shuffle_RMSE_CV) %>%
   mutate(CV = TRUE)) %>%
    gather(type, RMSE, -c(run_time, CV))
model_comp_observed <- model_comp %>%
    filter(type == "observed") %>%
   unnest(cols = c(RMSE))
model_comp_shuffle <- model_comp %>%
    filter(type == "shuffle") %>%
   unnest(cols = c(RMSE))
```

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.
- 353 URL: http://hdl.handle.net/2027.42/156251
- Allen, D. & Kim, A. Y. (2020), 'A permutation test and spatial cross-validation approach
- to assess models of interspecific competition between trees', PLOS ONE 15(3), e0229930.
- Publisher: Public Library of Science.
- URL: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0229930
- Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-
- Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer,

- J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin,
- S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K.,
- Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D. L.,
- Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert,
- G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B.
- C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M.,
- Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D.,
- Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X.,
- Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi,
- Y., Marthews, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R.,
- Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong,
- P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L.,
- Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W.,
- Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L.,
- Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X.,
- Weiblen, G., Wolf, A., Xu, H., Yap, S. & Zimmerman, J. (2015), 'CTFS-ForestGEO: a
- worldwide network monitoring forests in an era of global change', Global Change Biology
- **21**(2), 528–549.
- URL: http://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12712
- Bache, S. M. & Wickham, H. (2020), magrittr: A Forward-Pipe Operator for R. R package
- version 2.0.1.
- URL: https://CRAN.R-project.org/package=magrittr
- Bivand, R. S., Pebesma, E. & Gomez-Rubio, V. (2013), Applied spatial data analysis with
- R, Second edition, Springer, NY.
- URL: https://asdar-book.org/
- Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C. & Shen, X. (2013), 'Initial

- census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large
- Forest Dynamics Plot', *Ecology* **94**(9), 2111–2112.
- URL: http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/13-0010.1
- Canham, C. D., LePage, P. T. & Coates, K. D. (2004), 'A neighborhood analysis of canopy
- tree competition: effects of shading versus crowding', Canadian Journal of Forest Re-
- search 34(4), 778–787. Publisher: NRC Research Press Ottawa, Canada.
- URL: https://cdnsciencepub.com/doi/abs/10.1139/x03-232
- Canham, C. D., Papaik, M. J., Uriarte, M., McWilliams, W. H., Jenkins, J. C.
- ³⁹⁴ & Twery, M. J. (2006), 'Neighborhood Analyses Of Canopy Tree Competi-
- tion Along Environmental Gradients In New England Forests', Ecological Applica-
- tions 16(2), 540–554. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-
- 0761%282006%29016%5B0540%3ANAOCTC%5D2.0.CO%3B2.
- Das, A. (2012), 'The effect of size and competition on tree growth rate in old-growth
- coniferous forests', Canadian Journal of Forest Research 42, 1983–1995.
- Davies, S. J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A., Anderson-
- Teixeira, K., Andrade, A., Arellano, G., Ashton, P. S., Baker, P. J., Baker, M. E.,
- Baltzer, J. L., Basset, Y., Bissiengou, P., Bohlman, S., Bourg, N. A., Brockelman, W. Y.,
- Bunyavejchewin, S., Burslem, D. F., Cao, M., Cárdenas, D., Chang, L.-W., Chang-Yang,
- 404 C.-H., Chao, K.-J., Chao, W.-C., Chapman, H., Chen, Y.-Y., Chisholm, R. A., Chu, C.,
- Chuyong, G., Clay, K., Comita, L. S., Condit, R., Cordell, S., Dattaraja, H. S., de
- Oliveira, A. A., den Ouden, J., Detto, M., Dick, C., Du, X., Álvaro Duque, Ediriweera,
- S., Ellis, E. C., Obiang, N. L. E., Esufali, S., Ewango, C. E., Fernando, E. S., Filip,
- J., Fischer, G. A., Foster, R., Giambelluca, T., Giardina, C., Gilbert, G. S., Gonzalez-
- Akre, E., Gunatilleke, I., Gunatilleke, C., Hao, Z., Hau, B. C., He, F., Ni, H., Howe,
- R. W., Hubbell, S. P., Huth, A., Inman-Narahari, F., Itoh, A., Janík, D., Jansen, P. A.,

- Jiang, M., Johnson, D. J., Jones, F. A., Kanzaki, M., Kenfack, D., Kiratiprayoon, S.,
- 412 Král, K., Krizel, L., Lao, S., Larson, A. J., Li, Y., Li, X., Litton, C. M., Liu, Y., Liu,
- S., Lum, S. K., Luskin, M. S., Lutz, J. A., Luu, H. T., Ma, K., Makana, J.-R., Malhi,
- Y., Martin, A., McCarthy, C., McMahon, S. M., McShea, W. J., Memiaghe, H., Mi,
- X., Mitre, D., Mohamad, M., Monks, L., Muller-Landau, H. C., Musili, P. M., Myers,
- J. A., Nathalang, A., Ngo, K. M., Norden, N., Novotny, V., O'Brien, M. J., Orwig,
- D., Ostertag, R., Papathanassiou, K., Parker, G. G., Pérez, R., Perfecto, I., Phillips,
- R. P., Pongpattananurak, N., Pretzsch, H., Ren, H., Reynolds, G., Rodriguez, L. J.,
- Russo, S. E., Sack, L., Sang, W., Shue, J., Singh, A., Song, G.-Z. M., Sukumar, R., Sun,
- I.-F., Suresh, H. S., Swenson, N. G., Tan, S., Thomas, S. C., Thomas, D., Thompson,
- J., Turner, B. L., Uowolo, A., Uriarte, M., Valencia, R., Vandermeer, J., Vicentini, A.,
- Visser, M., Vrska, T., Wang, X., Wang, X., Weiblen, G. D., Whitfeld, T. J., Wolf, A.,
- Wright, S. J., Xu, H., Yao, T. L., Yap, S. L., Ye, W., Yu, M., Zhang, M., Zhu, D., Zhu, L.,
- Zimmerman, J. K. & Zuleta, D. (2021), 'Forestgeo: Understanding forest diversity and
- dynamics through a global observatory network', Biological Conservation 253, 108907.
- 426 URL: https://www.sciencedirect.com/science/article/pii/S0006320720309654
- Gonzalez-Akre, E., McGregor, I., Anderson-Teixeira, K., Dow, C., Herrmann, V., Terrell,
- A., Kim, A. Y., Vinod, N. & Helcoski, R. (2020), 'SCBI-ForestGEO/SCBI-ForestGEO-
- 429 Data: 2020 update'.
- 430 URL: https://doi.org/10.5281/zenodo.4041595
- 431 Gonzalez-Akre, E., Piponiot, C., Lepore, M. & Anderson-Teixeira, K. (2020), allodb: An
- R Database For Biomass Estimation At Extratropical Forest Plots. R package version
- 1.0.0.9000.
- 434 URL: https://qithub.com/forestgeo/allodb
- 435 Herring, J. R. (2011), OpenGIS implementation standard for geographic information-simple
- feature access part 1: Common architecture, Open Geospatial Consortium Inc., p. 211.

- Kuhn, M. & Wickham, H. (2020), Tidymodels: a collection of packages for modeling and
- machine learning using tidyverse principles.
- 439 URL: https://www.tidymodels.org
- 440 Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann,
- N. E., Kattge, J. & Coomes, D. A. (2012), 'Competitive interactions between forest
- trees are driven by species' trait hierarchy, not phylogenetic or functional similarity:
- implications for forest community assembly', *Ecology Letters* **15**(8), 831–840. Leprint:
- https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2012.01803.x.
- 445 URL: http://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2012.01803.x
- Lasky, J. R., Uriarte, M., Boukili, V. K. & Chazdon, R. L. (2014), 'Trait-mediated assembly
- processes predict successional changes in community diversity of tropical forests', Pro-
- ceedings of the National Academy of Sciences 111(15), 5616–5621. Publisher: National
- Academy of Sciences Section: Biological Sciences.
- URL: https://www.pnas.org/content/111/15/5616
- Pebesma, E. (2018), 'Simple Features for R: Standardized Support for Spatial Vector Data',
- The R Journal 10(1), 439–446.
- 453 URL: https://journal.r-project.org/archive/2018/RJ-2018-009/index.html
- Pohjankukka, J., Pahikkala, T., Nevalainen, P. & Heikkonen, J. (2017), 'Estimating the
- prediction performance of spatial models via spatial k-fold cross validation', *International*
- Journal of Geographical Information Science **31**(10), 2001–2019.
- Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauen-
- stein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A.,
- Hartig, F. & Dormann, C. F. (2017), 'Cross-validation strategies for data with temporal,
- spatial, hierarchical, or phylogenetic structure', *Ecography* **40**(8), 913–929.
- 461 URL: http://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.02881

- Silge, J. (2021), spatialsample: Spatial Resampling Infrastructure. R package version 0.1.0.
- URL: https://CRAN.R-project.org/package=spatialsample
- Smith, D. M. (1986), 'The practice of silviculture'.
- Smith, W. B. (2002), 'Forest inventory and analysis: a national inventory and monitoring
- program', Environmental pollution 116, S233–S242.
- Tatsumi, S., Owari, T. & Mori, A. S. (2016), 'Estimating competition coefficients in tree
- communities: a hierarchical bayesian approach to neighborhood analysis', Ecosphere
- 469 **7**, e01273.
- Team, G. D. (2017), GEOS geometry engine, open source, Open Source Geospatial Foun-
- dation, p. 211.
- 472 URL: https://trac.osgeo.org/geos/
- 473 Uriarte, M., Condit, R., Canham, C. D. & Hubbell, S. P. (2004), 'A spa-
- 474 tially explicit model of sapling growth in a tropical forest: does the iden-
- tity of neighbours matter?', Journal of Ecology 92(2), 348–360. _eprint:
- 476 https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.0022-0477.2004.00867.x.
- 477 URL: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.0022-
- 478 0477.2004.00867.x
- Uriarte, M., Swenson, N. G., Chazdon, R. L., Comita, L. S., Kress, W. J., Erickson, D.,
- Forero-Montana, J., Zimmeran, J. K. & Thompson, J. (2010), 'Trait similarity, shared
- ancestry and the structure of neighbourhood interactions in a subtropical wet forest:
- implications for community assembly', *Ecology Letters* **13**, 1503–1514.
- Valavi, R., Elith, J., Lahoz-Monfort, J. J. & Guillera-Arroita, G. (2019), 'blockCV: An
- r package for generating spatially or environmentally separated folds for k-fold cross-
- validation of species distribution models', Methods in Ecology and Evolution 10(2), 225—

- 232. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/2041-210X.13107.
- 487 URL: http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.13107
- Waller, L. A. & Gotway, C. A. (2004), Applied Spatial Statistics for Public Health Data,
- John Wiley & Sons, Incorporated, Hoboken, UNITED STATES.
- 490 URL: http://ebookcentral.proquest.com/lib/smith/detail.action?docID=214360
- Warmerdam, F. (2008), The Geospatial Data Abstraction Library, in G. B. Hall & M. G.
- Leahy, eds, 'Open Source Approaches in Spatial Data Handling', Advances in Geographic
- Information Science, Springer, Berlin, Heidelberg, pp. 87–104.
- Wickham, H. (2020), tidyr: Tidy Messy Data. R package version 1.1.2.
- 495 URL: https://CRAN.R-project.org/package=tidyr
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grole-
- mund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache,
- S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K.,
- Vaughan, D., Wilke, C., Woo, K. & Yutani, H. (2019), 'Welcome to the Tidyverse',
- Journal of Open Source Software 4(43), 1686.
- URL: https://joss.theoj.org/papers/10.21105/joss.01686