

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 11, 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

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 models of competition have been used to: test whether the species identity of a competitor matters [Uriarte et al. (2004); measure species-specific competition coefficients (Das 2012, Tatsumi et al. (2016)); test competing models to see what structures competitive interactions, e.g. traits or phylogeny (Allen & Kim 2020, Uriarte et al. 2010); and inform selective logging practices (Canham et al. 2006). Although these are well-described methods, few methods are currently available for easy application.

We address this shortcoming with the `forestecology` R package providing methods and data for forest ecology model fitting and assessment, available on CRAN (<https://cran.r-project.org/package=forestecology>) and on GitHub (<https://github.com/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).

Let $i = 1, \dots, n_j$ index all n_j trees of “focal” species j ; let $j = 1, \dots, J$ index all J focal species; and let $k = 1, \dots, K$ 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

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

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 $\beta_{dbh,j}$ 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 $\text{Normal}(0, \sigma^2)$.

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:

$$\begin{aligned} H_0 : \lambda_{jk} &= \lambda_j \text{ for all } k = 1, \dots, K \\ \text{vs. } H_A : &\text{at least one } \lambda_{jk} \text{ is different} \end{aligned} \tag{2}$$

Furthermore, to account for the spatial autocorrelation in their estimates of out-of-sample model error, Allen & Kim (2020) use spatial cross-validation. Estimates of model error that do not account for this dependence tend to underestimate the true model error (Roberts et al. 2017).

The package is designed with “tidy” design principles in mind (Wickham et al. 2019). Much like all **tidyverse** packages, **forestecology** has verb-named functions that can be modularly composed using the pipe `%>%` operator to sequentially complete all necessary analysis steps (Bache & Wickham 2020).

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:

¹See 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 simplified.

2 forestecology workflow: a case study

We present a case-study of `forestecology`’s functionality on data from the Smithsonian Conservation Biology Institute (SCBI) large forest dynamics plot in Front Royal, VA, USA, part of the ForestGEO global network of research sites (Bourg et al. 2013, Anderson-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 Ridge, Ridge and Valley, and Piedmont provinces—and is adjacent to the northern end of Shenandoah National Park.

The package has the following goals: to evaluate i) the effect of competitor species 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.
2. Add spatial information:
 1. Define a buffer region of trees.
 2. Add spatial cross-validation block information.

99 3. Identify all focal trees and their competitors.

100 4. Apply model, which includes:

101 1. Fit model.

102 2. Compute predicted values.

103 3. Visualize posterior distributions.

104 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
```

105 2.1 Step 1: Compute the growth of trees based on census data

106 We first compute the growth of trees using data from two censuses. `compute_growth()`
107 computes the average annual growth based on census data that roughly follows ForestGEO
108 standards. Despite such standards, minor variations will still exist between sites, thereby
109 necessitating some data wrangling. For example, the SCBI site records all DBH values in
110 millimeters (Bourg et al. 2013), whereas the Michigan Big Woods site used in Allen & Kim
111 (2020) records them in centimeters (Allen et al. 2020).

112 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))
```

117 These two data frames are then used as inputs to `compute_growth()`, along with `id`
118 specifying the variable that uniquely identifies each tree-stem. We also discard all resprouts
119 with `code == R` in the later census, since we are only interested in the growth of surviving,
120 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
##   <dbl> <fct> <dbl> <dbl> <dbl>   <POINT>
## 1      4 nysy  13.6  14.2  0.103 (14.2 428)
## 2      5 havi   8.8   9.6  0.150 (9.4 436)
## 3      6 havi   3.25   4    0.140 (1.3 434)
## 4     77 qual  65.2  66   0.141 (34.7 307)
## 5     79 tiam  47.7  46.8 -0.161 (40 381)
## # ... with 7,949 more rows

```

121 The output `growth_scbi` is a data frame of class `sf` that includes among other variables
 122 the species variable `sp` converted to a factor, the average annual `growth` in DBH ($\text{cm} \cdot$
 123 y^{-1}) for all stems that were alive at both time points, and the `sf` package's encoding of
 124 geolocations of geometry type `<POINT>`. Given that `growth_scbi` is of class `sf`, it can be
 125 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^{"

```

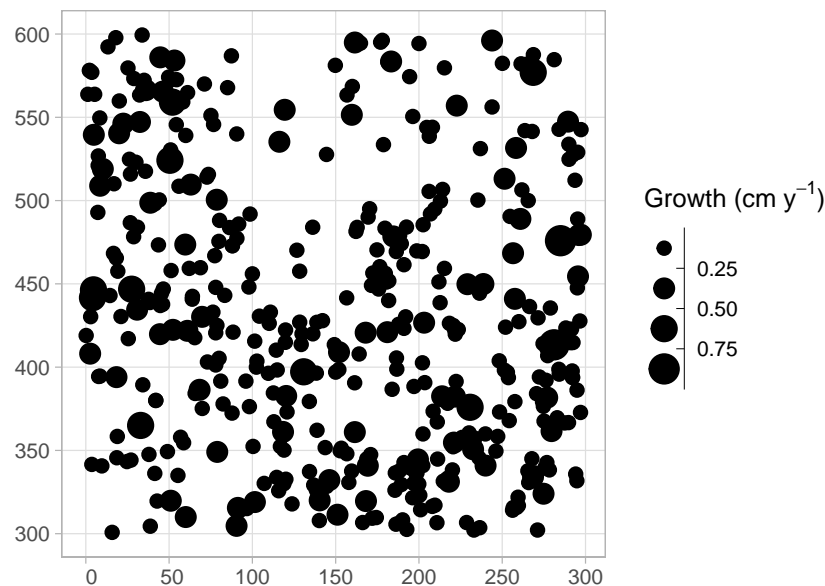



Figure 1: Step 1 - Compute growth of trees based on census data. A map of the growth of a random sample of 500 trees from a 9 ha subsection of the Smithsonian Conservation Biology Institute (SCBI) forest plot.

```

-1
}, ")))

```

126 We also load species information as it existed on GitHub on 2021/08/02, which in-
 127 cludes family, genus, and species information; as well as classifications of the canopy po-
 128 sition (canopy, canopy emergent, understory, shrub layer), drought tolerance (intolerant,
 129 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
##   sp      family      genus      species      canopy_position drought_toleran~
##   <chr> <chr>      <chr>      <chr>      <chr>          <chr>
## 1 acne  Sapindaceae  Acer       negundo     understory     drought-resista~

```

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

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

```
growth_scbi <- growth_scbi %>%
  left_join(sp_info, by = "sp") %>%
  mutate(sp = as.factor(sp))
```

132 Furthermore, we compute two potential competitor explanatory variables x_{ijk}^{comp} from
133 Equation 1. First, the basal area of each tree as a function of its DBH in the earlier
134 census. Second, the above ground biomass as estimated by allometric equations encoded
135 in the `get_biomass()` function from the `allodb` package (Gonzalez-Akre, Piponiot, Lepore
136 & Anderson-Teixeira 2020); this function has DBH, species, and geographic coordinates as
137 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)  
  )  
)
```

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 trees are: all trees within a distance `comp_dist` of a focal tree. Here we set `comp_dist` to 7.5m, a value informed by other studies (Canham et al. 2004, Uriarte et al. (2004), Canham et al. (2006)), but the package could also be used to compare multiple distances and see which is best supported (see Appendix A). We use `comp_dist` and a manually constructed `sf` representation of the study region’s boundary as inputs to `add_buffer_variable()` to add a `buffer` boolean variable to `growth_scbi`. All trees with `buffer` equal to `FALSE` will be our focal trees whose growth will be modeled, whereas those with `TRUE` will only act as competitor trees.

```
# 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)
```

155 The second element of spatial information we add are blocks corresponding to folds
156 of a spatial cross-validation algorithm. Conventional cross-validation algorithms assign
157 individual observations to folds by randomly resampling them all while assuming they are
158 statistically independent. In the case of forest census data however, observations exhibit
159 spatial autocorrelation. We therefore incorporate this dependence into the cross-validation
160 algorithm by resampling spatial blocks of trees (Roberts et al. 2017, Pohjankukka et al.
161 (2017)).

162 We first manually define an `sf` object defining four folds that partition the study region.
163 We then use the output of the `spatialBlock()` function from the `blockCV` package to
164 associate each tree in `growth_scbi` to the correct `foldID` (Valavi et al. 2019). This `foldID`
165 variable will be used in Section 2.6.

166 Figure 2 illustrates the net effect of adding these two elements of spatial information to
167 `growth_scbi`.

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

```
fold2 <- cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))
fold3 <- cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))
fold4 <- 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,
  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))
```

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

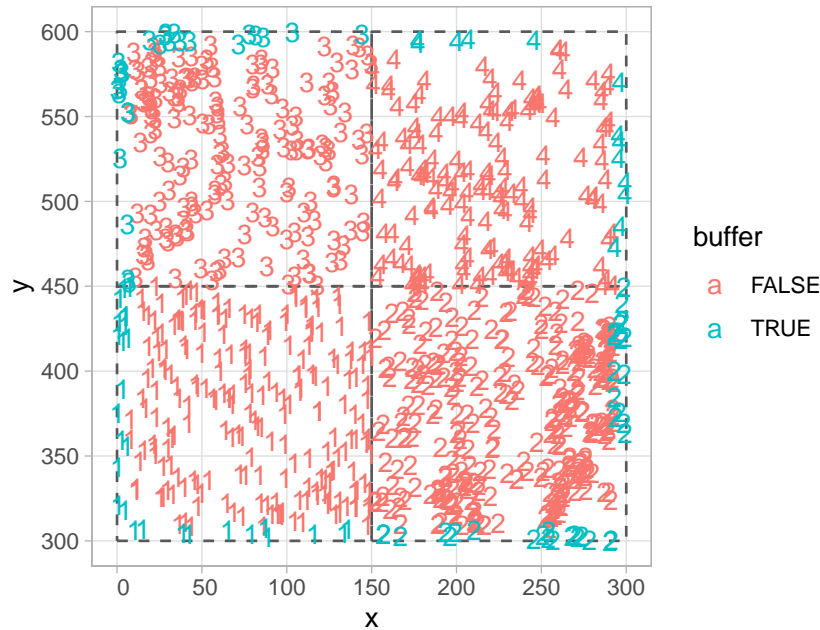


Figure 2: Step 2 - Add spatial information. A buffer region and spatial cross-validation blocks 1 through 4. The location of each tree is marked with its fold number where the folds are delineated with solid lines. The color of each digit indicates whether the tree is part of the buffer region (thus 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).

173 of the spatial cross-validation blocks `blocks_scbi`, and a specification `comp_x_var` of the
 174 `basal_area` variable we use as the competitor explanatory variable x_{ijk}^{comp} from Equation 1.
 175 This function returns a new data frame `focal_vs_comp_scbi`.

```
focal_vs_comp_scbi <- growth_scbi %>%
  create_focal_vs_comp(comp_dist, blocks = blocks_scbi, id = "stemID",
    comp_x_var = "basal_area")
focal_vs_comp_scbi %>%
  select(focal_ID, focal_sp, geometry, growth, comp)

## # A tibble: 6,296 x 5
##   focal_ID focal_sp   geometry growth comp
##   <dbl> <fct>       <POINT>   <dbl> <list>
## 1         4 nysy    (14.2 428)  0.103 <tibble [20 x 4]>
```

```
## 2      5 havi      (9.4 436)  0.150 <tibble [32 x 4]>
## 3     79 tiam      (40 381) -0.161 <tibble [20 x 4]>
## 4     80 caca      (38.7 422)  0.253 <tibble [12 x 4]>
## 5     96 libe      (60 310)  0.262 <tibble [14 x 4]>
## # ... with 6,291 more rows
```

176 The resulting `focal_vs_comp_scbi` has 6296 rows, representing the subset of the 7954
 177 trees in `growth_scbi` that will be considered as focal trees. The variables `focal_ID` and
 178 `focal_sp` relate to tree-stem identification and species information. Most notably however
 179 is the variable `comp`, which contains information on all competitor trees saved in `tidyr`
 180 package list-column format (Wickham 2020). To inspect this information, we flatten the
 181 `comp` list-column for the tree with `focal_ID` 4 in the first row, here a `tibble` [20 × 4],
 182 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
##   <dbl> <dbl> <dbl> <dbl> <fct>      <dbl>
## 1      4  13.6  1836  7.48 tiam      0.0176
## 2      4  13.6  1847  2.81 nysy      0.00332
## 3      4  13.6  1848  1.62 nysy      0.00396
## 4      4  13.6  1849  2.62 nysy      0.00535
## 5      4  13.6  1850  2.98 havi      0.00472
## # ... with 15 more rows
```

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

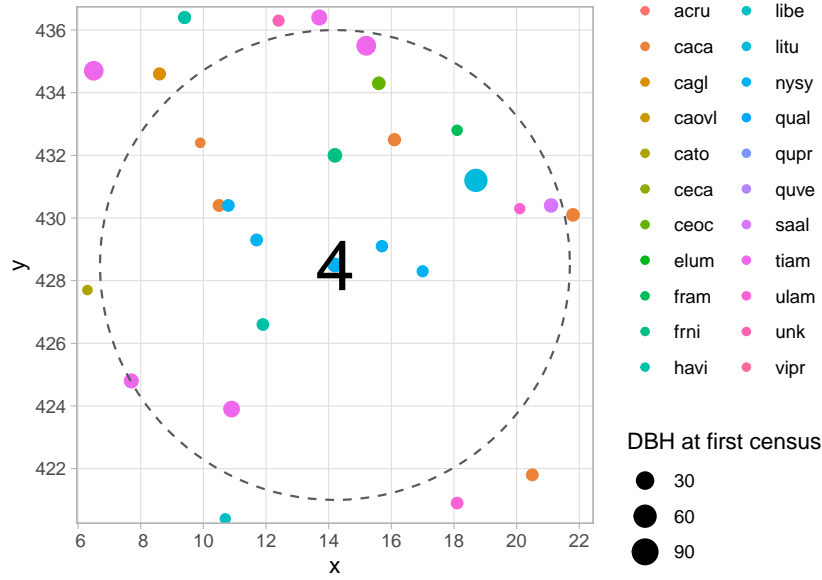


Figure 3: Step 3 - Identify all focal and corresponding competitor trees. The dashed circle extends 7.5m away from the focal tree 4 while all 20 competitor trees are within this circle.

distance to the focal tree (all $\leq 7.5\text{m}$), the species, and the basal area (in m^2) calculated as $\frac{\pi \times (\text{DBH}/2)^2}{10000}$ 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 package is flexible to allow the user to specify any competitor explanatory variable (basal area, biomass, tree height, a soil nutrient value, ...). The package can also be used to compare competitor explanatory variables and see which best explains tree growth, see Appendix B for an example comparing basal area and above ground biomass. Similarly, the package can use any categorical variable as an explanatory variable and compare between different categorical variables. For example in Allen & Kim (2020) we compare grouping individuals based on species, family, and based on trait-based groups. In Appendix C we give another example and compare grouping individuals by species or by potential canopy position (canopy, understory, shrub layer).

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    mu_star  
## 4 Multivariate t on beta  V_0     V_star  
##  
## Model formula:  
## growth ~ sp + dbh + dbh * sp + acne * sp + acru * sp + amar * sp + astr  
## * sp + caca * sp + caco * sp + cade * sp + cagl * sp + caoul * sp + cato  
## * sp + ceca * sp + ceoc * sp + chvi * sp + cofl * sp + crpr * sp + crsp  
## * sp + divi * sp + elum * sp + fagr * 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
```

206 Next, the generic for `predict()` takes the posterior parameter values in `comp_bayes_lm_scbi`
 207 and a `newdata` data frame, and outputs a vector `growth_hat` of predicted DBH values \widehat{y}_{ij}
 208 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
##   <dbl> <fct>   <dbl> <dbl>    <dbl>
## 1      4 nysy    13.6  0.103   0.0809
## 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
```

209 We can now compare the observed and predicted growths to compute the root mean
 210 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
```

211 Lastly, the generic for `ggplot2::autoplot()` allows us to visualize all posterior dis-
212 tributions, as seen in Figure 4. Setting `type` to "intercepts" and "dbh_slopes" returns
213 species-specific posterior distributions for $\beta_{0,j}$ and $\beta_{dbh,j}$ respectively, while setting `type =`
214 "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
```

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

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

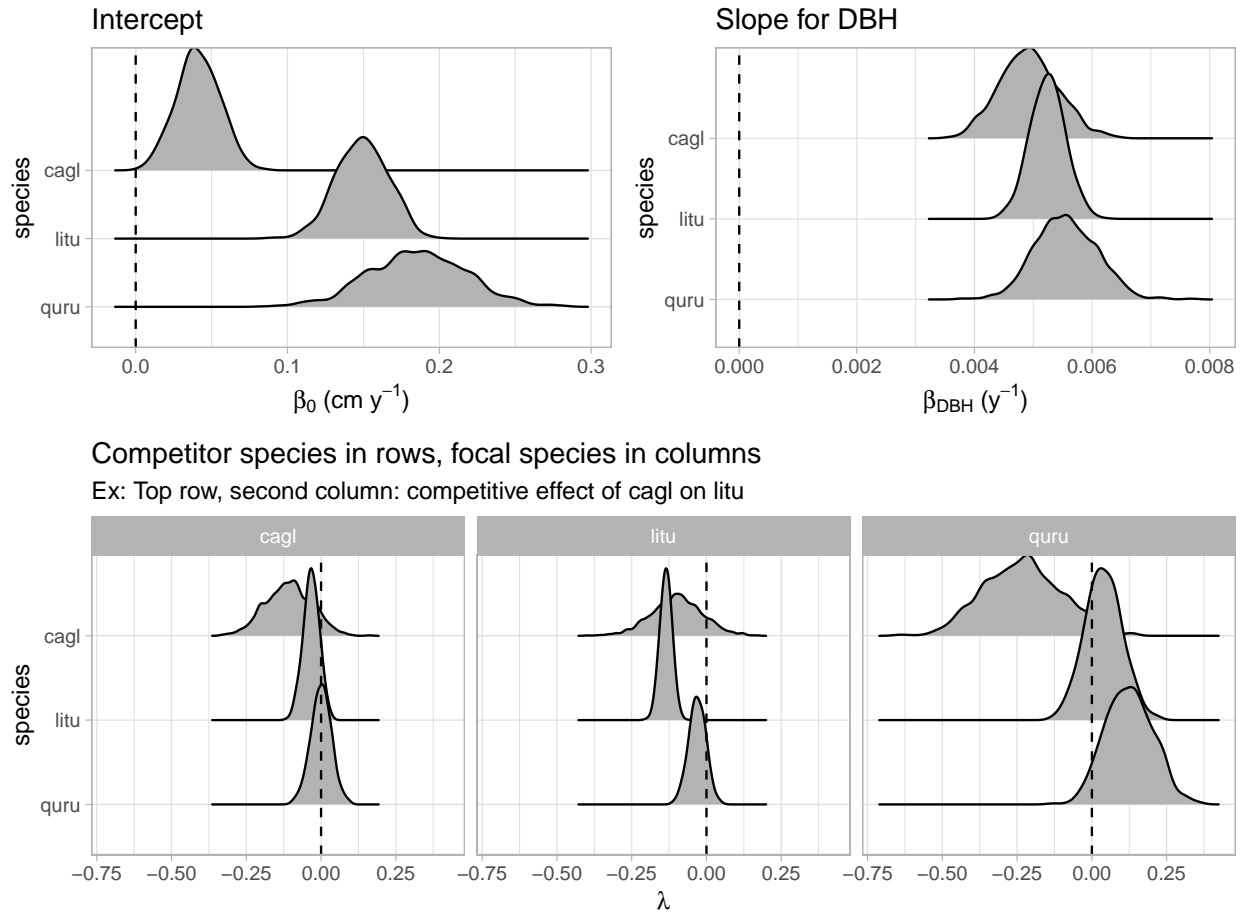


Figure 4: Step 4 - Fit model. Posterior distributions of all parameters. For compactness we include only three species.

implemented in a function similar to `comp_bayes_lm()`.

2.5 Evaluate the effect of competitor species identity using permutation tests

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

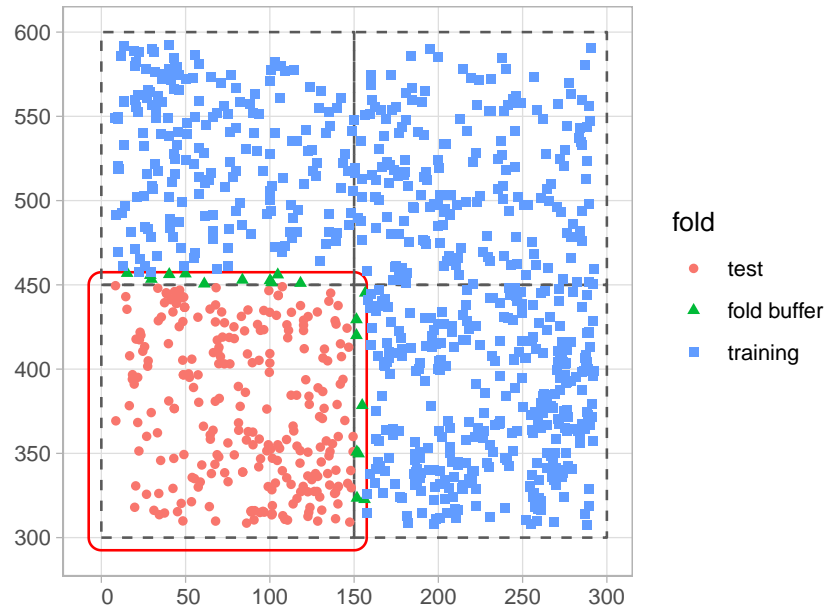


Figure 5: Schematic of spatial cross-validation. Using the $k = 1$ fold (bottom-left) as the test set, $k = 2$ through 4 as the training set, along with a fold buffer extending outwards from the test set to maintain spatial independence between it and the training set.

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).

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

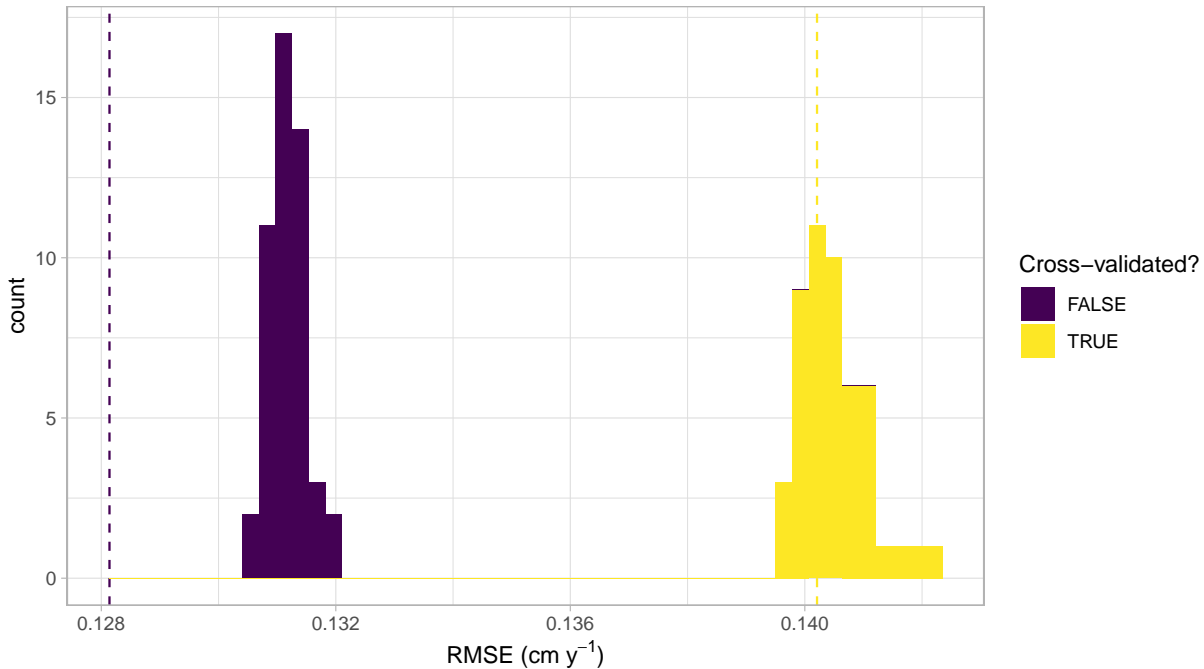


Figure 6: Comparison of root mean squared error of models for standard, permuted, and spatially cross-validated error estimates. The dotted lines show observed RMSE while the histograms show the null distribution of RMSE for 49 permutations under the null hypothesis of no competitor species identity 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.

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 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> (Gonzalez-Akre, 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(

  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 <- cbind(c(200, 400, 400, 200), c(0, 0, 200, 200))
fold3 <- cbind(c(0, 200, 200, 0), c(200, 200, 400, 400))
fold4 <- cbind(c(200, 400, 400, 200), c(200, 200, 400, 400))

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  
  )  
  
growth_scbi <- growth_scbi %>%  
  mutate(foldID = spatial_block_scbi$foldID %>% factor())  
  
mult_dist_comp <- tibble(  
  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]  
  
  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", cor  
    run_cv(comp_dist = comp_dist, blocks = blocks_scbi)  
  
  mult_dist_comp$rmse[i] <- focal_vs_comp_scbi %>%
```

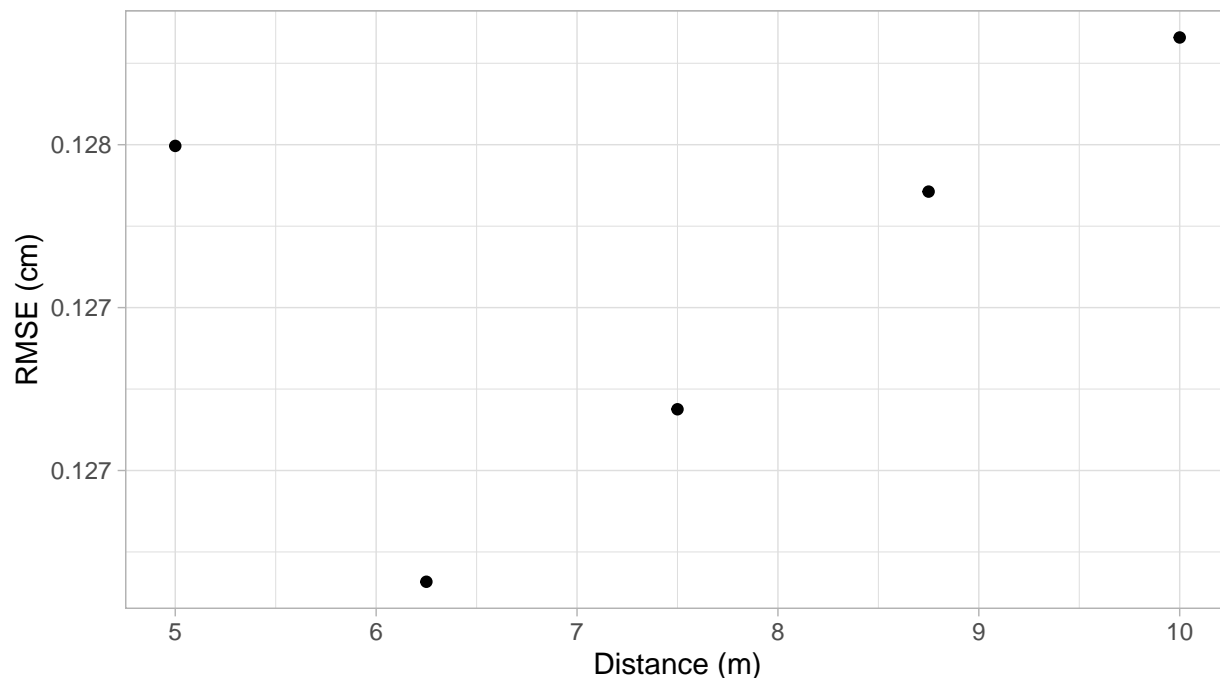


Figure 7: Cross-validated RMSE estimates for 5 competitive distances.

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

B Appendix: Compare competitor explanatory variables

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(  
    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 <- 4  
  
fold1 <- cbind(c(0, 150, 150, 0), c(300, 300, 450, 450))  
fold2 <- cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))  
fold3 <- cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))  
fold4 <- 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,
  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
```

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

336 C Appendix: Compare grouping variables

337 The package also allows the user to specify the categorical explanatory grouping variable.
338 Here we compare two different such variables: species and the potential canopy position of
339 that species. If we had individual-level crown classes (Smith (1986) dominant, codominant,
340 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))
```

```
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) %>%  
  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_scbi) %>%  
  filter(!str_detect(codes, "R")), id = "stemID") %>%  
  left_join(sp_info, by = "sp") %>%  
  mutate(canopy_position = str_replace(canopy_position, " ", "_"), canopy_position = str_replace(canopy_position, ",", ""))  
  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 <- cbind(c(0, 150, 150, 0), c(300, 300, 450, 450))  
fold2 <- cbind(c(150, 300, 300, 150), c(300, 300, 450, 450))  
fold3 <- cbind(c(0, 150, 150, 0), c(450, 450, 600, 600))  
fold4 <- 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,
  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") %>%
```

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

focal_vs_comp_can_pos <- growth_scbi_can_pos %>%
  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_sp %>%
  rmse(truth = growth, estimate = growth_hat) %>%
  pull(.estimate)
## [1] 0.14

focal_vs_comp_can_pos %>%
  rmse(truth = growth, estimate = growth_hat) %>%
  pull(.estimate)
## [1] 0.144
```

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

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

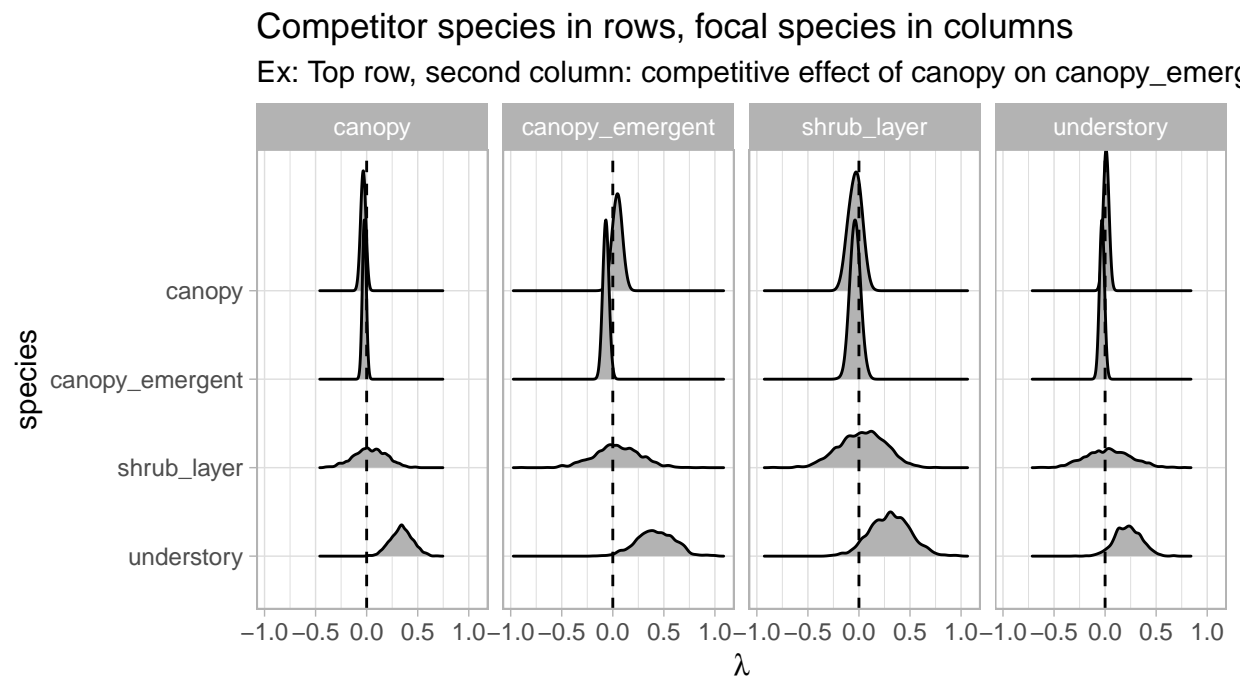


Figure 8: Posterior distributions of all competition parameters.

```
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 <- 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))
n_fold <- 4

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
SpatialBlock_scbi <- spatialBlock(speciesData = growth_scbi, k = n_fold,
  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)
shuffle_RMSE_CV <- vector("list", 1)
filename <- here("paper/simulation_results/") %>%
  str_c("2021-03-03_scbi_", num_shuffle, "_shuffles")

# Run all simulations 0. 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)
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)

# 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)
run_time <- clock$toc - clock$tic

model_comp_tbl <- tibble(run_time = run_time, observed_RMSE = observed_RMSE,
  observed_RMSE_CV = observed_RMSE_CV, shuffle_RMSE = shuffle_RMSE, shuffle_RMSE_CV =
  )

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))
```

```

cv_plot <- ggplot() + geom_vline(data = model_comp_observed, aes(xintercept = RMSE,
  col = CV), linetype = "dashed", show.legend = F) + geom_histogram(data = model_comp.
  aes(x = RMSE, fill = CV), bins = 50) + labs(fill = "Cross-validated?",
  x = expression(paste("RMSE (cm ", y^{
    -1
  }, ")))) + scale_color_viridis(discrete = TRUE, option = "D") + scale_fill_viridis
  theme_light()
cv_plot

filename %>%
  str_c(".pdf") %>%
  ggsave(plot = cv_plot, width = 16/2, height = 9/2)

```

References

- Allen, D., Dick, C., Burnham, R. J., Perfecto, I. & Vandermeer, J. (2020), ‘The Michigan Big Woods research plot at the Edwin S. George, Pinckney, MI, USA’, *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **207**.
URL: <http://hdl.handle.net/2027.42/156251>
- 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 Research* **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. & Twery, M. J. (2006), ‘Neighborhood Analyses Of Canopy Tree Competition Along Environmental Gradients In New England Forests’, *Ecological Applications* **16**(2), 540–554. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-0761%282006%29016%5B0540%3ANAOTC%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, 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., 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.

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-Data: 2020 update'.

URL: <https://doi.org/10.5281/zenodo.4041595>

Gonzalez-Akre, E., Pioniot, 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.

URL: <https://github.com/forestgeo/allodb>

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*.

URL: <https://www.tidymodels.org>

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. [eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2012.01803.x](https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2012.01803.x).

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’, *Proceedings 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.

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., Guillerá-Arroita, G., Hauenstein, 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.

URL: <http://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.02881>

- 462 Silge, J. (2021), *spatialsample: Spatial Resampling Infrastructure*. R package version 0.1.0.
463 **URL:** <https://CRAN.R-project.org/package=spatialsample>
- 464 Smith, D. M. (1986), ‘The practice of silviculture’.
- 465 Smith, W. B. (2002), ‘Forest inventory and analysis: a national inventory and monitoring
466 program’, *Environmental pollution* **116**, S233–S242.
- 467 Tatsumi, S., Owari, T. & Mori, A. S. (2016), ‘Estimating competition coefficients in tree
468 communities: a hierarchical bayesian approach to neighborhood analysis’, *Ecosphere*
469 **7**, e01273.
- 470 Team, G. D. (2017), GEOS - geometry engine, open source, Open Source Geospatial Foun-
471 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-
475 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-](http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.0022-0477.2004.00867.x)
478 [0477.2004.00867.x](http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.0022-0477.2004.00867.x)
- 479 Uriarte, M., Swenson, N. G., Chazdon, R. L., Comita, L. S., Kress, W. J., Erickson, D.,
480 Forero-Montaña, J., Zimmeran, J. K. & Thompson, J. (2010), ‘Trait similarity, shared
481 ancestry and the structure of neighbourhood interactions in a subtropical wet forest:
482 implications for community assembly’, *Ecology Letters* **13**, 1503–1514.
- 483 Valavi, R., Elith, J., Lahoz-Monfort, J. J. & Guillera-Aroita, G. (2019), ‘blockCV: An
484 r package for generating spatially or environmentally separated folds for k-fold cross-
485 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>.

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.

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.

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>