

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

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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 demonstrate that both i) competitor species identity matters and ii) that not spatially cross-validating leads to error estimates that are overly optimistic.

4. The package features i) **tidyverse**-like structure whereby verb-named functions 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

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the Bayesian linear regression model. These three facts allow for clear articulation of all the steps in the sequence of analysis and easy wrangling and visualization of the geospatial forestry data. Furthermore, while the package only has Bayesian linear regression implemented, the package was designed with extensibility to other methods in mind.

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

1 Introduction

Repeat-censused forest plots offer excellent data 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) Tattsumi 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, no methods are currently available for their easy application. Here we address this in an R package. We largely follow the methods presented in Allen & Kim (2020). The package is written to model stem radial growth between two censuses based on neighborhood competition. It assumes a single large plot using the ForestGEO plot data structure as a guide (Anderson-Teixeira et al. (2015)).

Allen & Kim (2020) considers the following model: Let $i = 1, \dots, n_j$ index all n_j trees of “focal” species group j ; let $j = 1, \dots, J$ index all J focal species groups; and let $k = 1, \dots, K$ index all K “competitor” species groups. We model the average annual growth in diameter y_{ij} (in centimeters per year) of the i^{th} tree of focal species group j as a linear model f of the covariates \vec{x}_{ij}

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

where $\beta_{0,j}$ is the diameter-independent growth rate for group j ; dbh_{ij} is the diameter at breast height (in centimeters) of the focal tree at the earlier census; $\beta_{dbh,j}$ is the amount of the growth rate changed depending on diameter for group j ; BA_{ijk} is the sum of the basal area of all trees of competitor species group k ; λ_{jk} is the change in growth for individuals of group j from nearby competitors of group k ; and ϵ_{ij} is a random error term distributed Normal($0, \sigma^2$). They estimate all parameters via Bayesian linear regression while exploiting

Normal/Inverse Gamma conjugacy to derive closed-form solutions to all posterior distributions via linear algebra¹. These closed-form solutions for the posterior distributions are in contrast to approximations of all posteriors via computationally expensive Markov Chain Monte Carlo algorithms.

In order to evaluate whether competitor species identity matters, Allen & Kim (2020) run a permutation test where under the null hypothesis the species identity of all competitors of a focal tree can be permuted/shuffled:

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

$$\text{vs. } H_A : \text{at least one } \lambda_{jk} \text{ is different} \quad (3)$$

where the null hypothesis H_0 reflects a hypothesis of no species grouping-specific effects of competition while the alternative hypothesis H_A reflects a hypothesis of species grouping-specific effects of competition. Furthermore, in order to account for the spatial autocorrelation inherent to forest data 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 spatial dependency tend to underestimate the true model error (Roberts et al. 2017).

We introduce the `forestecology` R package providing methods and data for forest ecology model fitting and assessment, available on CRAN (<https://cran.r-project.org/web/packages/forestecology/index.html>) with the corresponding source code available on GitHub (<https://github.com/rudeboybert/forestecology>). The package implements all aspects of the model in Equation 1: model fitting and generating fitted/predicted values, evaluating the effect of competitor species identity using permutation tests, and evaluating model performance using spatial cross-validation.

¹See S1 Appendix of Allen & Kim (2020), available at <https://doi.org/10.1371/journal.pone.0229930.s004>

The package designed with “tidy” design principles in mind (Wickham et al. 2019). Much like many of the **tidyverse** component packages, **forestecology** is designed with verb-named functions that can be modularly composed in sequence using the pipe `%>%` operator (Bache & Wickham 2020). As we articulate in Section 2, these functions delineate the key steps in our analysis sequence. Furthermore, the inputs and outputs of nearly all of our functions use the same “simple features for R” data structures as implemented in the **sf** package for standardized support for spatial vector data (Pebesma 2018). The **sf** package is a **tidyverse**-friendly evolution of the **sp** package of classes and methods for spatial data in R (Pebesma & Bivand 2005). As such, wrangling and visualization spatial data such as ours becomes much easier.

Currently the package only implements the Bayesian linear regression model of tree growth based on neighborhood competition detailed in Equation 1. As we demonstrate in Section 2.4 however, the fitting of this model is self-contained in a single function `comp_bayes_lm()`. This function returns an object of S3 class type `comp_bayes_lm` with generic methods implemented for `print()` to inspect the output, `predict()` to generate fitted/predicted values, and `ggplot2::autoplot()` to visualize all results. Therefore the package can be modularly extended to fit other models as long as they are coded into a function similar type as `comp_bayes_lm()` as has equivalent generic methods implemented.

We present a case-study of the **forestecology** package’s use on data from the Smithsonian Conservation Biology Institute’s (SCBI) large forest dynamics plot in Front Royal, Virginia, USA in Section 2, which is part of the ForestGEO global network of research sites (Bourg et al. 2013, Anderson-Teixeira et al. (2015)). The package is designed with ForestGEO plot data in mind, but we envision that it could easily be modified to work with data from other forest plots, e.g. the US Forest Service Forest Inventory and Analysis plots or more generally to model interactions of any community of mapped sessile organisms (Smith 2002).

2 forestecology workflow: a case study

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

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

1. Compute the growth of stems based on two censuses.

2. Add spatial information:

1. Define a buffer region of trees.

2. Add spatial cross-validation block information.

3. Identify all focal trees and their competitors.

4. Apply model, which includes:

1. Fit model.

2. Compute fitted/predicted values.

3. Visualize posterior distributions.

127 We start by loading all necessary packages.

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

128 2.1 Step 1: Compute the growth of trees based on census data

129 {compute-growth}

130 The first step in the our analysis sequence is to compute the growth of trees using data from
131 two censuses. The `compute_growth()` function computes average annual growth assuming
132 census data that roughly follows ForestGEO standards. Despite such standards, minor
133 variations will still exist between sites, thereby necessitating some data wrangling and
134 checking. For example, the SCBI site records all diameters at breast height (DBH) in
135 millimeters (Bourg et al. 2013), whereas the Michigan Big Woods site records them in
136 centimeters (Allen et al. 2020).

137 We load both 2008 and 2014 SCBI census data `.csv` files as they existed on GitHub on
138 November 20, 2020 (Gonzalez-Akre et al. 2020). After selecting only the relevant variables,
139 we perform a few additional data wrangling steps: convert the character variable with
140 the date of measurement to be of explicit type `date`, convert DBH to be in centimeters²
141 Furthermore, in order to speed up computation for purposes of this example, we only
142 consider a 9 ha subsection of the 25.6 ha of the SCBI site: `gx` from 0–300 instead of 0–400
143 and `gy` from 300–600 instead of 0–640.

²A rule of thumb to determine the units of DBH is to check if the smallest non-zero and non-missing measurement is 1 or 10. If the former, then centimeters. If the later, then millimeters. This is because ForestGEO protocols state that only trees with DBH greater or equal to 1cm should be included in censuses.

```
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))
```

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

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



```

growth_scbi
## Simple feature collection with 7954 features and 8 fields
## geometry type:  POINT
## dimension:      XY
## bbox:           xmin: 0.2 ymin: 300 xmax: 300 ymax: 600
## CRS:            NA
## # A tibble: 7,954 x 9
##   stemID sp      dbh1 codes1 status  dbh2 codes2 growth  geometry
##   <dbl> <fct> <dbl> <chr>  <chr>  <dbl> <chr>  <dbl>  <POINT>
## 1      4 nysy  13.6  M      A      14.2 M      0.103 (14.2 428)
## 2      5 havi   8.8  M      A      9.6 M;P    0.150 (9.4 436)
## 3      6 havi   3.25 NULL  A      4      M      0.140 (1.3 434)
## 4     77 qual  65.2  M      A     66      M      0.141 (34.7 307)
## 5     79 tiam  47.7  M      A     46.8 M     -0.161 (40 381)
## # ... with 7,949 more rows

```

The output `growth_scbi` is a single data frame of class `sf` that includes variables `growth`, the average annual growth in DBH (cm y^{-1}) for all stems that were alive at both time points, and `geometry`, the `sf` package's encoding of geolocations of type `<POINT>`. In addition the species variable `sp` is converted to a factor if it wasn't already by `compute_growth()`.³ Furthermore, the variables that should remain unchanged between censuses appear only once, such as location variables `gx` and `gy`; as well as species-related variables. Variables that should change between censuses are suffixed with 1 and 2 indicating the earlier and later censuses, such as `dbh1/dbh2` and `codes1/codes2`.

Site data that does not align with this convention will need to be transformed for use

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

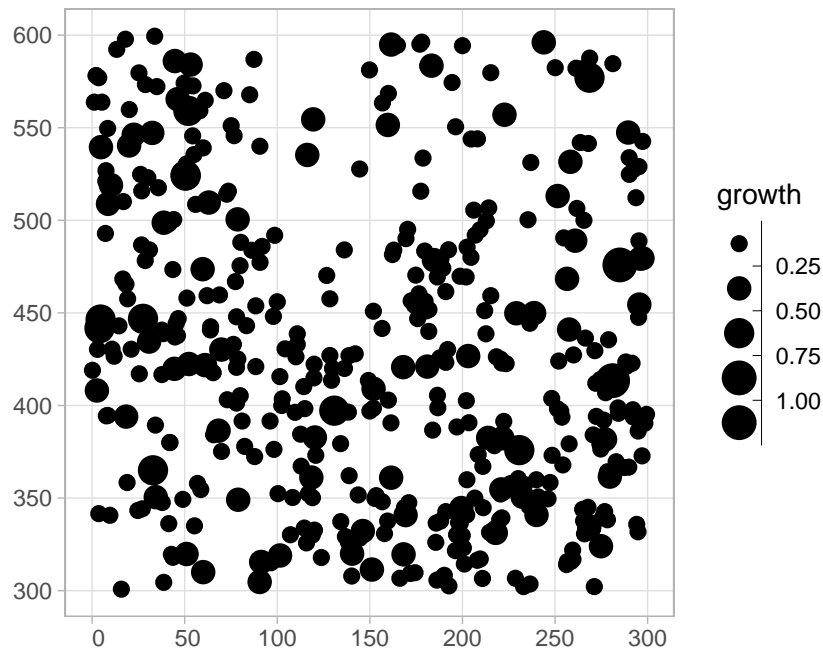


Figure 1: Compute growth of trees based on census data: Map with growth of a random sample of 500 trees from a 9 ha subsection of the Smithsonian Conservation Biology Institute (SCBI) forest plot.

with the `compute_growth()` function. However, in the end, all that matters is that the growth of all stems is saved in a data frame of class `sf` and, at a minimum, contains the variable uniquely identifying each stem, `sp`, `dbh1`, `growth`, `geometry`.

Given that `growth_scbi` is of class `sf`, it can be easily plotted in `ggplot2` using the `geom_sf()` geometry as seen in Figure 1 where we plot a random sample of 500 out of the 7954 trees.

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

2.2 Step 2: Add spatial information

The next step in our analysis sequence is to add additional spatial information to our main `growth_scbi` data frame. The first element of spatial information we add is a “buffer region”

to the periphery of the study region. Since some of our model's explanatory variables are cumulative (such as competitor basal area), we must ensure that all trees being modeled are not biased to have different neighbor structures. This is of concern for trees at the boundary of study regions, for which all neighbors will not be included in the censused stems. In order to account for such edge effects, only trees that are not part of this buffer region, i.e. are part of the interior of the study region, will have their growth modeled (Waller & Gotway 2004).

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

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

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

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

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

```
# Manually define spatial blocks to act as folds  
n_fold <- 4  
fold1 <- rbind(c(0, 300), c(150, 300), c(150, 450), c(0, 450))  
fold2 <- rbind(c(150, 300), c(300, 300), c(300, 450), c(150, 450))  
fold3 <- rbind(c(0, 450), c(150, 450), c(150, 600), c(0, 600))  
fold4 <- rbind(c(150, 450), c(300, 450), c(300, 600), c(150, 600))  
  
blocks_scbi <- bind_rows(  
  sf_polygon(fold1), sf_polygon(fold2), sf_polygon(fold3),  
  sf_polygon(fold4)  
) %>%
```

⁴In the Supporting Information we present an example where the folds themselves are also created using the `spatialBlock()` function given a specified `cv.block.size`.

```
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())
```

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

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

201 2.3 Step 3: Identify all focal and corresponding competitor trees

202 The next step in our analysis sequence is to identify all focal trees and their corresponding
203 competitor trees. More specifically, it identifies all trees that are not part of the buffer
204 region, have a valid `growth` measurement, and have at least one neighbor within 7.5 of it.

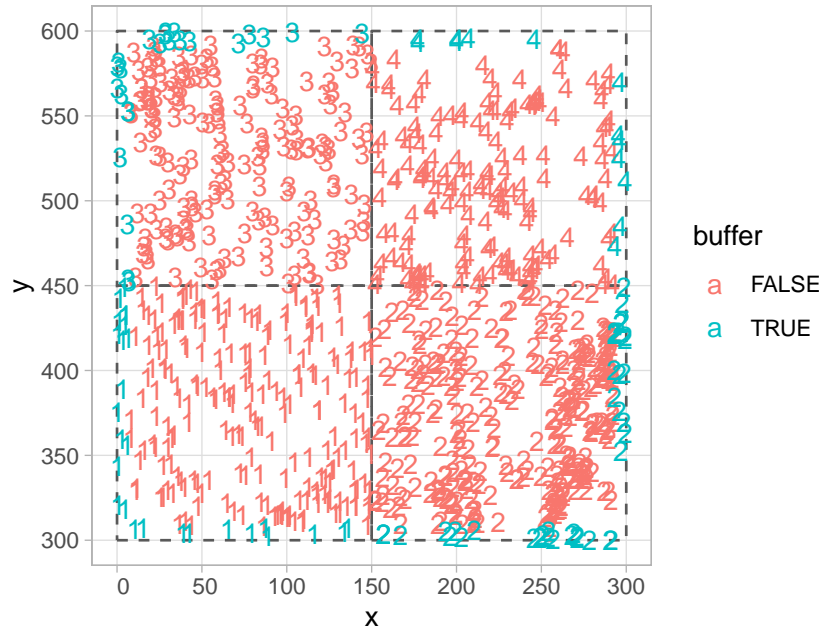


Figure 2: Add spatial information: Buffer region and spatial cross-validation blocks (1 through 4). All trees in the interior of the study region (i.e. not part of buffer) will be the focal trees whose growth will be modeled.

The `create_focal_vs_comp()` function performs these tasks and returns a new data frame of type `sf`. On top of the previous arguments `comp_dist` defining the competition neighborhood and `id` indicating which variable uniquely identifies each tree-stem, this function also requires an `sf` object representation of the spatial cross-validation blocks/folds. In this example, the blocks were manually encoded in `blocks_scbi` by specifying its vertices in Section 2.2⁵. We present the resulting data frame below with the `foldID` variable omitted for compactness of presentation.

```
focal_vs_comp_scbi <- growth_scbi %>%
  create_focal_vs_comp(comp_dist, blocks = blocks_scbi, id = "stemID")
focal_vs_comp_scbi %>%
  select(-foldID)

## # A tibble: 6,296 x 6
```

⁵We present an alternative method for defining spatial cross-validation blocks is using the `spatialBlock()` function from the `blockCV` package in the Supporting Information.

```
##   focal_ID focal_sp   dbh   geometry growth comp
##   <dbl> <fct>    <dbl>    <POINT>  <dbl> <list>
## 1      4 nysy     13.6 (14.2 428)  0.103 <tibble [20 x 4]>
## 2      5 havi      8.8 (9.4 436)  0.150 <tibble [32 x 4]>
## 3     79 tiam     47.7 (40 381) -0.161 <tibble [20 x 4]>
## 4     80 caca      5.15 (38.7 422)  0.253 <tibble [12 x 4]>
## 5     96 libe      2.3  (60 310)  0.262 <tibble [14 x 4]>
## # ... with 6,291 more rows
```

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

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

219 The spatial distribution of these trees is visualized in Figure 3: the dashed circle extends
 220 7.5 m away from the focal tree while all 20 competitor trees are within this circle.

221 Using the `unnest()` function from the `tidyr` package, we can flatten list-column into

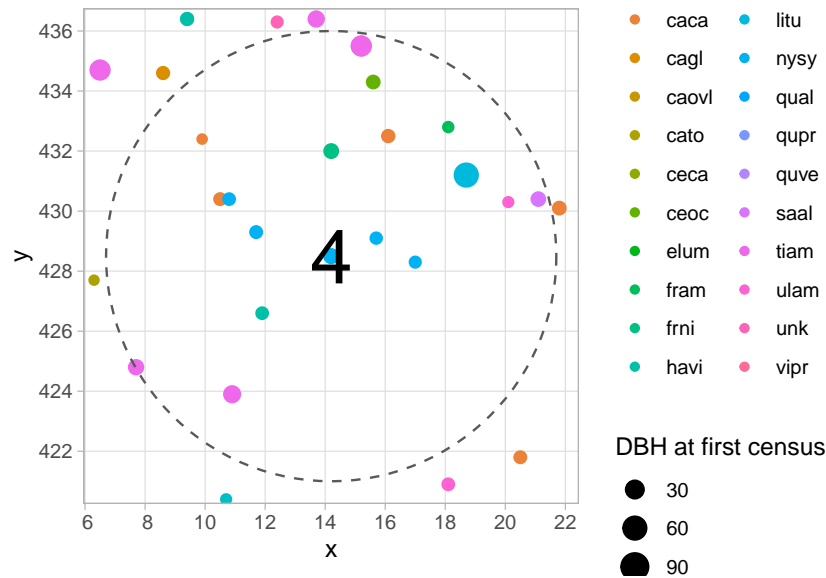


Figure 3: Identify all focal and corresponding competitor trees: All 20 competitor trees of focal tree 4.

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

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

## # A tibble: 20 x 6
##   focal_ID  dbh comp_ID  dist comp_sp comp_basal_area
##   <dbl> <dbl>   <dbl> <dbl> <fct>         <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
```

2.4 Step 4: Fit model

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

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

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

```
comp_bayes_lm_scbi
## Bayesian linear regression model parameters with a multivariate Normal likelihood.
##
##      parameter_type      prior posterior
```

```
## 1 Inverse-Gamma on sigma^2 a_0 a_star
## 2 Inverse-Gamma on sigma^2 b_0 b_star
## 3 Multivariate t on beta mu_0 mu_star
## 4 Multivariate t on beta V_0 V_star
##
## Model formula:
## growth ~ sp + dbh + dbh * sp + acne * sp + acru * sp + amar * sp + astr * sp + caca
```

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

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

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

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

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

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

```
# Plot posteriors for only a subset of species  
sp_to_plot <- c("litu", "quru", "cagl")  
  
plot1 <- autoplot(comp_bayes_lm_scbi, type = "intercepts",  
  sp_to_plot = sp_to_plot)  
plot2 <- autoplot(comp_bayes_lm_scbi, type = "dbh_slopes",  
  sp_to_plot = sp_to_plot)  
plot3 <- autoplot(comp_bayes_lm_scbi, type = "competition",  
  sp_to_plot = sp_to_plot)  
  
# Combine plots using patchwork  
(plot1 | plot2) / plot3
```

250 These plots give the posterior distributions of parameters from Equation 1. For many
251 package users they will be of interest because they give insight into the species-specific
252 competitive interactions. Setting `type = "intercepts"` gives posterior distributions for
253 $\beta_{0,j}$ and `type = "dbh_slopes"` for $\beta_{dbh,j}$. These give species specific growth independent of
254 competition. The values of more interest are plotted with `type = 'competition'` which
255 gives the posterior distribution for $\lambda_{j,k}$ species-specific competition coefficients (i.e., the

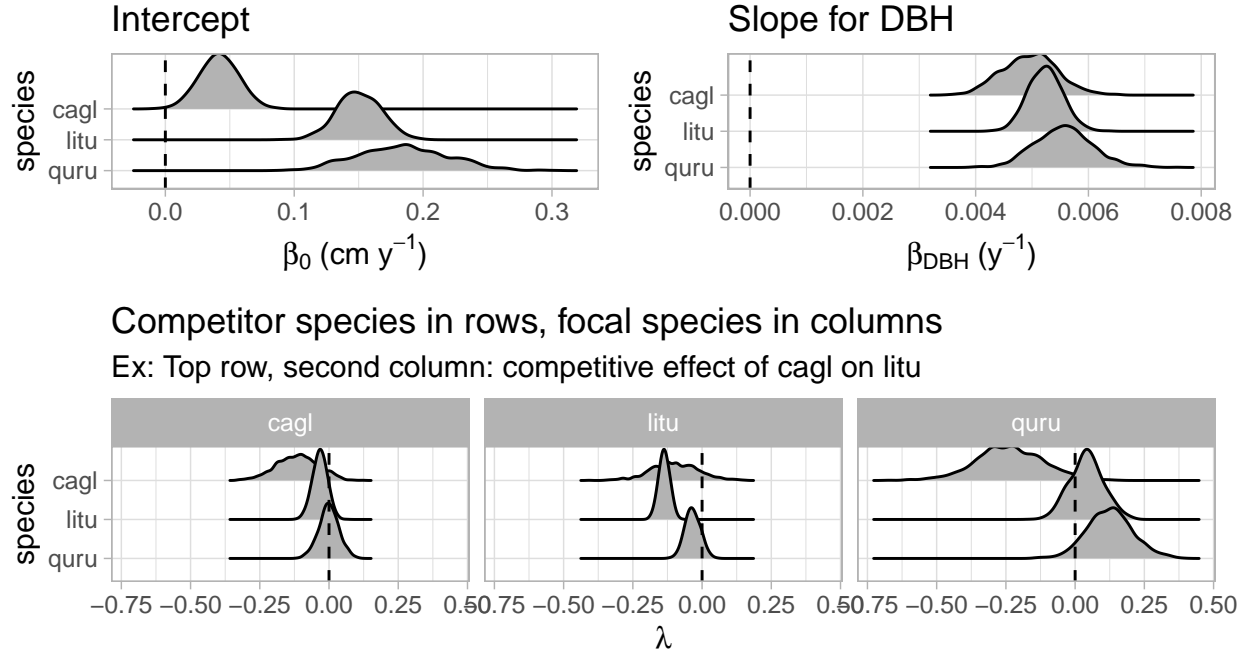


Figure 4: Fit model: Posterior distributions of all parameters for three species.

λ -matrix). Negative values indicate a competitor species which slows the growth of a focal species. Here, for example, we see that tulip trees (`litu`) have a strong negative effect on the growth of conspecifics but relatively little effect on neighbors of the other two species.

2.5 Evaluate the effect of competitor species identity using permutation tests

In order to evaluate the effect of competitor species identity, we use the four steps of our analysis sequence answer along with a permutation test: Under a null hypothesis where competitor species identity does not matter, we can permute/shuffle this variable within each focal tree, compute the RMSE (the test statistic of interest), repeat this process several times to construct a null distribution of the RMSE, and compare it to the observed RMSE 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 randomly resamples the `comp_sp` variable with replacement, leaving all other variables intact. The resampling with replacement is nested

269 within each focal tree in order to preserve the neighborhood structure of our competition
270 model. To run the permutation test, we use the same `comp_bayes_lm()` function as in
271 Section 2.4, but with a `run_shuffle = TRUE` argument.

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

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

272 The resulting RMSE of 0.131 based on the permutation test is larger than the earlier
273 RMSE of 0.128, suggesting that models that do incorporate competitor species identity
274 better fit the data. We conduct an analysis of the full SCBI plot in Section 3 below.

275 2.6 Evaluate model performance using spatial cross-validation

276 We answer the second of our two questions: how can we obtain an accurate estimate of
277 model performance/error? The model fits and predictions in Section 2.4 all suffer from a
278 common failing: they use the same data to both fit the model and to assess the model's
279 performance using the RMSE. As argued by Roberts et al. (2017), this can lead to overly

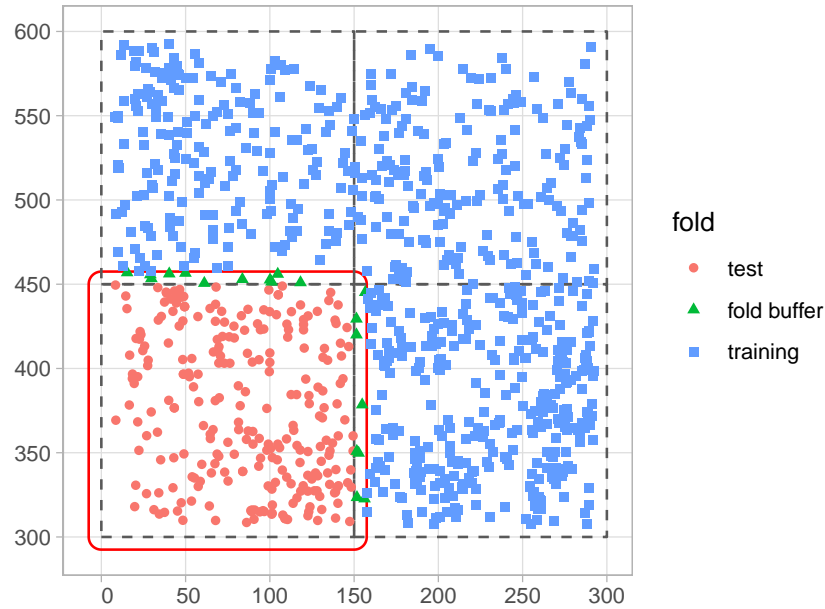


Figure 5: Schematic of spatial cross-validation: Using the $k = 1$ fold as the test set, assigning each focal tree to training set, test set, and fold buffer.

optimistic assessments of model quality as the models can be overfit, in particular in situations where spatial-autocorrelation is present. To mitigate the effects of such overfitting, we use a spatially block cross-validation algorithm.

To this end, we use the `foldID` variable defined in Section 2.2 whereby all focal trees are assigned to one of 4 spatially contiguous blocks that act as folds in our cross-validation routine. Figure 5 presents a schematic illustrating this scheme for fold 1 (bottom-left) as the test set and folds 2, 3, and 4 as the training sets. We fit the model to all focal trees in the training set, apply the model to all focal trees in the test set to compute fitted/predicted values, and compute the RMSE of the observed versus predicted growths. We repeat this procedure 3 more times with each of the three remaining folds acting as the test set and then average all four resulting RMSE's. Furthermore, in order to maintain spatial independence between the test and training set, a fold buffer that extend outwards from the boundary of the test set is computed; all trees falling within this fold buffer are excluded from the training set.

This algorithm is implemented in the `run_cv()` function, which is a wrapper function to

the `comp_bayes_lm()` function that fits the model and the `predict()` generic that returns fitted/predicted values. We compare these values to the observed growth values to again compute our RMSE.

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

```
model_rmse_cv <- focal_vs_comp_scbi %>%  
  rmse(truth = growth, estimate = growth_hat) %>%  
  pull(.estimate)  
model_rmse_cv  
## [1] 0.14
```

The resulting RMSE of 0.14 computed using cross-validation is larger than the earlier RMSE of 0.128, suggesting that models that do not take the inherent spatial autocorrelation of the data into account generate error estimates that are overly optimistic; in our case RMSE's that are too low. We conduct an analysis of the full SCBI plot in Section 3 below.

3 Results

Figure 6 highlights the importance of spatial cross validating when interpreting results from neighborhood competition models. Without cross-validation the competitor identity did matter, the non-permuted competitor species had a much lower RMSE than the permuted one. But once we include the spatial cross validation this improvement disappears. So in this 9 ha subplot of the SCBI plot competitive interactions do not depend on the identity of the competitor, which is the opposite of what has been observed in other places (Allen & Kim (2020) Uriarte et al. (2004)).

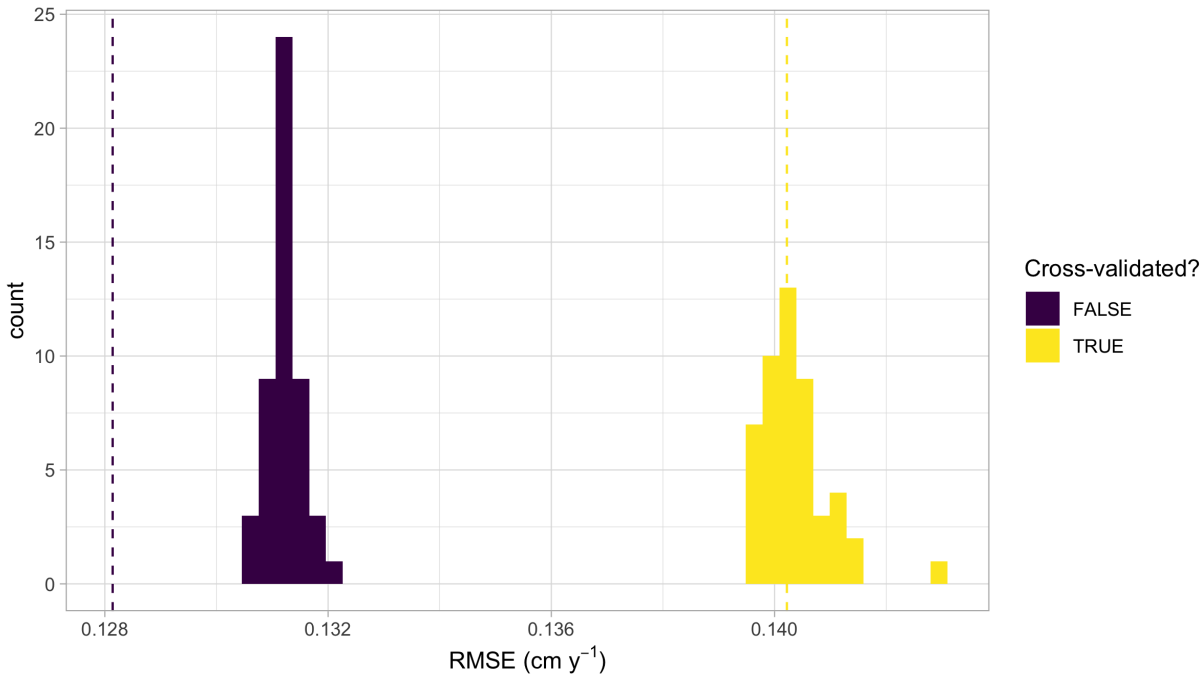


Figure 6: Root mean squared error of models for standard, permuted, and spatial cross-validated error estimates.

4 Conclusion

The `forestecology` package provides an accessible way to fit and test models of neighborhood competition. Currently it is written to work with data from ForestGEO plots. But it could easily be modified to work on any single large, mapped forest plot in which at least two measurements of each individual have been taken. With a little bit of work the package could also be applied to forest inventory data in which several small plots are spatially separated, e.g., USFS Forest Inventory. In a future version of the package we also hope to make it possible to model plant mortality in addition to plant growth. The package follows the guidelines for `tidy` data, `sf` spatial structure, and S3 open-oriented model structure. These make for ease of use. We hope that the package will further the use of neighborhood competition models to better understand what structures plant competition.

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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 the forestecology package as well as this manuscript on GitHub at <https://github.com/rudeboybert/forestecology>. This repository will be versioned and archived on Zenodo upon acceptance. The 2008 and 2014 Smithsonian Conservation Biology Institute census data loaded in Section ?? and saved in `scbi.stem2.csv` and `scbi.stem3.csv` are available on GitHub at https://github.com/SCBI-ForestGEO/SCBI-ForestGEO-Data/tree/master/tree_main_census/data/census-csv-files and have been versioned and archived on Zenodo at <https://doi.org/10.5281/zenodo.2649301> (Gonzalez-Akre et al. 2020).

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*

342 *Publications of the Museum of Zoology, University of Michigan* **207**.

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

344 Allen, D. & Kim, A. Y. (2020), ‘A permutation test and spatial cross-validation approach
345 to assess models of interspecific competition between trees’, *PLOS ONE* **15**(3), e0229930.

346 Publisher: Public Library of Science.

347 **URL:** <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0229930>

348 Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-
349 Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer,
350 J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin,
351 S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K.,
352 Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D. L.,
353 Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert,
354 G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B.
355 C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M.,
356 Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D.,
357 Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X.,
358 Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi,
359 Y., Marthens, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R.,
360 Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong,
361 P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L.,
362 Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W.,
363 Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L.,
364 Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X.,
365 Weiblen, G., Wolf, A., Xu, H., Yap, S. & Zimmerman, J. (2015), ‘CTFS-ForestGEO: a
366 worldwide network monitoring forests in an era of global change’, *Global Change Biology*

367 **21**(2), 528–549.

368 **URL:** <http://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12712>

369 Bache, S. M. & Wickham, H. (2020), *magrittr: A Forward-Pipe Operator for R*. R package
370 version 2.0.1.

371 **URL:** <https://CRAN.R-project.org/package=magrittr>

372 Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C. & Shen, X. (2013), ‘Initial
373 census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large
374 Forest Dynamics Plot’, *Ecology* **94**(9), 2111–2112.

375 **URL:** <http://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/13-0010.1>

376 Canham, C. D., LePage, P. T. & Coates, K. D. (2004), ‘A neighborhood analysis of canopy
377 tree competition: effects of shading versus crowding’, *Canadian Journal of Forest Re-*
378 *search* **34**(4), 778–787. Publisher: NRC Research Press Ottawa, Canada.

379 **URL:** <https://cdnsiencepub.com/doi/abs/10.1139/x03-232>

380 Canham, C. D., Papaik, M. J., Uriarte, M., McWilliams, W. H., Jenkins, J. C.
381 & Twery, M. J. (2006), ‘Neighborhood Analyses Of Canopy Tree Competi-
382 tion Along Environmental Gradients In New England Forests’, *Ecological Applica-*
383 *tions* **16**(2), 540–554. eprint: [https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-](https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-0761%282006%29016%5B0540%3ANAOTC%5D2.0.CO%3B2)
384 [0761%282006%29016%5B0540%3ANAOTC%5D2.0.CO%3B2](https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-0761%282006%29016%5B0540%3ANAOTC%5D2.0.CO%3B2).

385 Das, A. (2012), ‘The effect of size and competition on tree growth rate in old-growth
386 coniferous forests’, *Canadian Journal of Forest Research* **42**, 1983–1995.

387 Gonzalez-Akre, E., McGregor, I., Anderson-Teixeira, K., Dow, C., Herrmann, V., Terrell,
388 A., Kim, A. Y., Vinod, N. & Helcoski, R. (2020), ‘SCBI-ForestGEO/SCBI-ForestGEO-
389 Data: 2020 update’.

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

- 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>
- Pebesma, E. J. & Bivand, R. S. (2005), ‘Classes and methods for spatial data in R’, *R News* **5**(2), 9–13.
URL: <https://CRAN.R-project.org/doc/Rnews/>
- 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>
- 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* **7**, e01273.
- Uriarte, M., Condit, R., Canham, C. D. & Hubbell, S. P. (2004), ‘A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter?’, *Journal of Ecology* **92**(2), 348–360. [_eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.0022-0477.2004.00867.x](https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.0022-0477.2004.00867.x)
URL: <http://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.0022-0477.2004.00867.x>

- Uriarte, M., Swenson, N. G., Chazdon, R. L., Comita, L. S., Kress, W. J., Erickson, D.,
Forero-Montaña, 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](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>
- 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>