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Presence-absence sampling for estimating plant density using survey data with variable plot size

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Abstract

1. Presence-absence sampling is an important method for monitoring state and change of both individual plant species and communities. With this method only the presence or absence of the target species is recorded on plots and thus the method is straightforward to apply and less prone to surveyor judgement compared to other vegetation monitoring methods. However, in the basic setting all plots must be equally large or otherwise it is unclear how data should be analyzed. In this study we propose and evaluate five different methods for estimating plant density based on presence-absence registrations from surveys with variable plot sizes.

2. Using artificial plant population data as well as empirical data from the Swedish National Forest Inventory we evaluated the performance of the proposed methods. The main analysis was conducted through sampling simulation in the artificial populations, whereby bias and variance of density estimators for the different methods were quantified and compared.

3. Both for state and change estimation of plant density, we found that the best method to handle variable plot size was to perform generalized least squares regression, using plot size as an independent variable. Methods where plots smaller than a certain threshold were excluded or their registrations recalculated were, however, almost as good. Using all registrations as if they were obtained from plots with the nominal plot size resulted in substantial bias.

4. Our findings are important for plant population studies in a wide range of environmental monitoring programmes. In these programmes plots are typically randomly laid out and may be located across boundaries between different land use or land cover classes, resulting in subplots of variable size. Such splitting of plots is common when large plots are used, e.g. with the 100 m^2 plots used in the Swedish National Forest Inventory. Our methods overcome problems to estimate plant density from presence-absence data observed in plots that vary in size.

Keywords: vegetation survey, divided plots, quadrats, plant monitoring, Poisson model, point pattern, plant density, intensity

Introduction

Vegetation surveys are becoming increasingly important due to society's increasing interest in ecosystem services linked to different vegetation types (Lindenmayer and Likens 2010; Yapp *et al.* 2010). For example, several large-scale forest and landscape inventories have included detailed vegetation assessment components in their protocols (e.g. Corona *et al.* 2011, Ståhl *et al.* 2011). However, contrary to monitoring trees and forests, monitoring non-tree vegetation offers substantial methodological challenges (Elzinga *et al.* 1998; Godínez-Alvarez *et al.* 2009). One common method is based on assessing the cover of individual species or species groups on plots through ocular inspection. In several studies, this method has been shown to be susceptible to substantial surveyor-induced bias (e.g. Kercher *et al.* 2003; Morrison 2016). Line- and grid point intercept methods (Godínez-Alvarez *et al.* 2009) involve detailed species recordings at randomly selected points. Such methods are less prone to surveyor judgement, but typically require large sample sizes and are thus costly to conduct.

Presence-absence sampling is another routinely employed method for surveying individual plants or vegetation communities (e.g. Bonham 2013). Compared to the other methods, it is straightforward to apply since it requires only registrations of presences or absences of species on plots. This method is often less prone to surveyor judgement compared to cover assessment (e.g. Kercher *et al.* 2003; Ringvall *et al.* 2005), although with large plots the variability between surveyors may still be substantial (Milberg *et al.* 2008). A drawback is that state and change of plant occurrence frequencies are difficult to interpret due to their dependence on plot size and species occurrence patterns. Thus, several studies suggest that frequency should be recalculated to plant density (Royle and Nichols 2003; He and Reed 2006; Hwang and He 2011; Ståhl *et al.* 2017). Such recalculation depends on model assumptions about the species occurrence patterns. A straightforward and commonly adopted assumption is the Poisson model (e.g., Bonham 2013), which stipulates entirely random locations of individuals. However, many species tend to occur in clustered patterns and thus other spatial processes have been explored as well (e.g. Hwang and He 2011).

To use presence-absence sampling effectively, the plot size need to be fixed or otherwise the probabilities of plant occurrence will vary between plots and the results will depend on the size distribution of the plots, unless variability in plot size is considered in the computations. However, to our knowledge, no theory seems to exist for handling variable plot sizes in connection with presence-absence sampling. A common ad-hoc approach is to set a size threshold below which all plots are excluded from the analysis (e.g. Odell and Ståhl 1998).

Due to its simplicity, the presence-absence survey method is applied in several monitoring programmes (e.g. Tomppo *et al.* 2010). However, in many monitoring programmes (e.g. Fridman *et al.* 2014) the random distribution of plots implies that the plot sizes may vary. The reason is that plots are sometimes divided into subplots by land use or land cover boundaries (Fig. 1), or that parts of plots cannot be occupied by plants, e.g. due to disturbances, rocks or boulders.

Figure 1. An illustration of how land use and land cover boundaries may incur variable plot sizes in presence-absence sampling when plots are allocated randomly across a study landscape (in this case in a randomly located square cluster system). The plots with yellow parts are divided between different land use or land cover categories, and each part must be surveyed separately when results by land cover type or land use category are required.

The objective of this study was to propose and evaluate five different methods for analyzing sample plot data with variable plot sizes from surveys based on presence-absence sampling, when the goal is to estimate state and change in plant density. The methods are (i) using data without modifications (our baseline method), (ii) removing all plots smaller than a certain threshold size from the analysis, (iii) re-computing presence-absence registrations on plots smaller than the nominal size by adding a modelled presence probability; i.e. an “absence plot” may become a “presence plot”, (iv) allocating each plot to a specific size class followed by separate computations for each size class and then merging the results, and (v) using regression analysis to predict the probability of species occurrence on a plot, including plot size as a predictor variable and plant density as a parameter to be estimated.

Throughout the article we use the term *density* for the average number of plants per area unit rather than the synonym *intensity*, which is commonly used in spatial statistics.

Materials and Methods

Plant population data

Two different datasets were utilized in the study. The first set was obtained through simulation of occurrences of a hypothetical plant species in artificial landscapes, assuming different plant densities and spatial patterns. In these landscapes, sample surveys were simulated and the performance of the different methods for handling variable plot size evaluated. The second dataset consisted of empirical observations from the Swedish National Forest Inventory (NFI).

Artificial plant population data

Three cases of artificial plant population data were simulated, each with subcases:

- *Case I*: Plant occurrences within the study landscape followed a homogeneous Poisson process, i.e. the plants were located entirely at random in the landscape. Three subcases were distinguished by different plant densities: (a) 0.005, (b) 0.01, and (c) 0.02 plants m^{-2}. According to Ståhl et al. (2017), the optimum plot size to use for assessing plant density at a true plant density of 0.016 plants m^{-2} is 100 m^{2}. Thus, we chose plant densities in this order of magnitude for the analyses. Case I is our baseline case where the plant densities are the same across the entire artificial landscapes.

- *Case II*: Plant occurrences within the landscape followed the Poisson model, but with different densities in different strata. Four different strata were assumed to be present in the landscape, each with the same area proportion, i.e. 25%. The stratum-level plant densities were 0.005, 0.008, 0.011, and 0.014 plants m^{-2}. Two subcases were distinguished: (a) stratum identifiers were available and the differences between strata could be accounted for, and (b) stratum identifiers were not available. Thus, *Case IIb* resembles Case *IIa* with regard to average plant density, but in *IIb* the density varies across the landscape in a way that cannot be utilized in the analysis. Case II was introduced to mimic more realistic plant populations, compared to the baseline.

- *Case III*: This case is similar to *Case II* (incl. the subcases), but plant densities close to boundaries were different compared to the interior densities. The plant densities were doubled within a 10 m wide zone on both sides along all stand boundaries. This implies that the average plant densities were higher in *Case III* compared to *Case II*. Case III was introduced for assessing the sensitivity of the proposed methods to more complicated situations, with dependencies between plot size and plant density. Other similar cases could have been analyzed as well, but our ambition was not to analyze all possible cases. Our focus was to generically address more complicated population structures, compared to *Case I* and *Case II*.

Each simulated artificial landscape consisted of 500 square forest stands. For Case II and Case III each stand was assigned to a specific stratum.

We used landscapes with three different stand sizes to study how the different methods' ability to handle variable plot size would be affected by the proportion of divided plots, and thus the degree of size variability among the plots. The intuition is that small stands imply that a large proportion of the landscape area will be located close to boundaries and thus a large proportion of the plots will be divided, since all plots extending across stand boundaries were divided and only the larger subplots were retained in the analysis. The stand areas studied were (i) 0.15 ha resulting in about 50% of the plots being divided (denoted *small stands*), (ii) 0.7 ha resulting in about 25% of the plots being divided (denoted *intermediate stands*), and (iii) 4.8 ha resulting in about 10% divided plots (denoted *large stands*). Thus, the total area of the study landscape varied depending on stand size, but this does not affect the results of the analysis. For Case III, the 10 m boundary zones with higher plant densities corresponded to about 77%, 42% and 17%, respectively, of the total landscape area for the three stand size types.

As an illustration, Fig. 2 shows a part of a simulated landscape (Case III with large stands) with plant locations marked as circles.

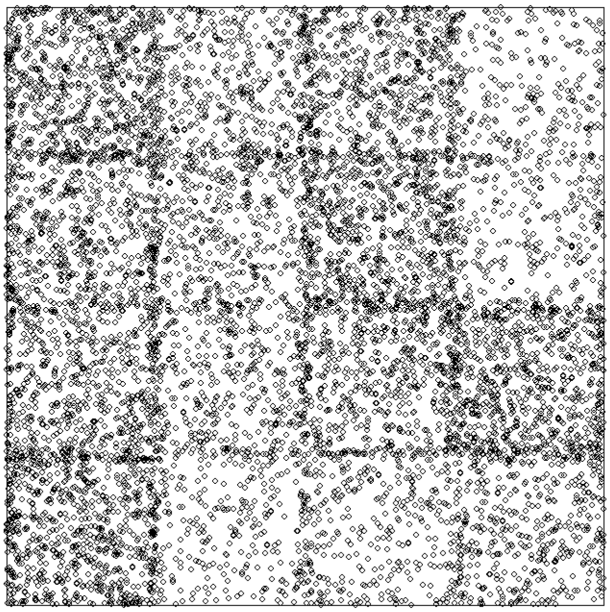

Figure 2. An example of a part of an artificial landscape with different plant densities in different stands (depending on what stratum a stand belongs to). The example shows Case III with large stands. Individual plants are displayed as circles.

Thus, a large number of artificial landscapes with different stand sizes and plant occurrence patterns (according to the three cases) were constructed as a basis for subsequent sampling simulations to assess the performance of the different methods for handling variable plot size. The details of the sampling simulations are described separately, further down.

Empirical plant population data

The Swedish NFI uses 0.25 m^2 and 100 m^2 circular plots for presence-absence registrations of forest floor vegetation (Fridman *et al.* 2014). In this study, the 100 m^2 plots were used, since they are often divided between land-use categories or forest types, and for practical reasons presence-absence registrations are only conducted on one part of divided plots (the larger subplot). Moreover, due to disturbances or occurrence of substrates on which the target species cannot grow, such as rocks and boulders, the potential growing space of a species on a plot may be smaller than the nominal plot size; the extent of such areas is recorded on the plots. Forest floor vegetation is assessed every 10 years on permanent plots in the NFI (Fridman *et al.* 2014). The NFI data were used mainly for illustrating differences in estimates when the five methods for handling variable plot sizes were applied on real data. In this case, we could not compare the results with a true value, as in the case of artificial data.

Data from the NFI were retrieved for the years 2011 to 2015 from two large regions within Sweden (regions 2 and 4 according to the NFI; Fig. 3) for the forest age class 20-60 years. Data for two species were included: *Trientalis europaea (L.) and Melampyrum pratense (L.).* A summary of the NFI data is provided in Table 1, displaying the number of plots in different size categories. It can be noted that 12% and 21% of the plots were divided in region 2 and 4, respectively, i.e. for these plots the plot size was smaller than the nominal 100 m^2.

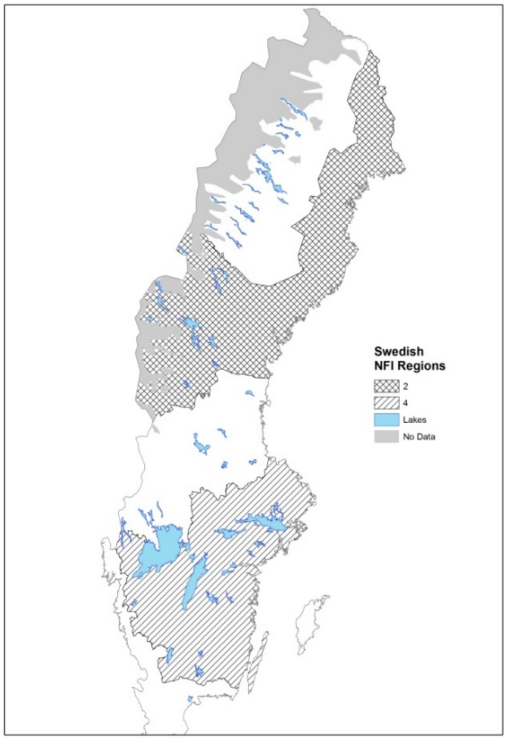

Figure 3. A map of Sweden and the locations of the National Forest Inventory regions 2 and 4, which were selected for the study.

Table 1. Number of sample plots in different size classes in the two study regions

Size class (m^2)	*Region 2*	*Region 4*
0-19	13	10
20-39	16	37
40-59	23	90
60-79	69	134
80-99	78	201
100	1409	1762
Total	1608	2234

Evaluating methods for handling variable plot size

In standard application of presence-absence sampling the plot size needs to be fixed or otherwise the results will depend on the specific mix of plot sizes, which complicates the interpretation of results (cf. the modifiable areal unit problem, e.g. Jelinski and Wu (1996), in geography). In making use of frequency data, the state and change of frequencies are typically reported (for a given nominal plot size) or the frequencies are recomputed to plant density. To compute density from frequency, assuming that the plant locations follow a Poisson model, we note that the probability, *p*, that at least one plant will occur on a plot with size *a* is (e.g. Ståhl *et al.* 2017)

$$p = 1 - e^{-a\lambda} \qquad (1)$$

where λ is the plant density. For a sample survey using *n* plots, *p* can be estimated as $\hat{p} = n^{-1}\sum_{i=1}^{n} I_i$, where I_i is an indicator variable that takes the value 1 if the species is present on plot *i* and 0 otherwise. Rearranging (1), we can estimate plant density from the proportion of plots with plant occurrences as (e.g. Ståhl *et al.* 2017)

$$\hat{\lambda} = -\frac{\ln(1-\hat{p})}{a} \qquad (2)$$

From (2) it is clear that the plot size must be fixed or otherwise it is unclear how the estimation of plant density should be conducted.

In this study we propose and evaluate five different methods for handling variable plot size in surveys with presence-absence registrations. The methods are:

(i) Use the presence-absence data without correction and apply the nominal plot size in all computations, even if the actual average plot area is smaller due to, e.g., some of the plot being divided. This is our baseline approach in which no attempt is made to adjust for the effect of variable plot size. This method is denoted *BASELINE*.

(ii) A size threshold is implemented and all plots with a smaller size are discarded from the analysis, i.e. some plots (smaller than the nominal size) are removed from the dataset when this method is applied. Two different size thresholds were implemented in the study: (a) 90% and (b) 60% of the nominal plot size. This method is denoted *THRESHOLD*; the notation THRESHOLD90 is used for the size threshold 90% and the notation THRESHOLD60 for the threshold 60%.

(iii) Plots with presences are included without correction regardless of plot size while a recalculation is made for plots with absences, if they are smaller than the nominal size, so that a plot may shift to being registered as a plot with presences. The intuition is that a plant of the target species might have occurred on the plot, if the plot would have had the full nominal size. The recalculation is based on the probability that at least one plant would occur on the missing plot area (i.e. the nominal area minus the actual area) under a Poisson model assumption, estimated using plots with the nominal size only. A random number is selected for determining whether or not the registration for a plot should change from absence to presence. This method is denoted *RECALCULATION*.

(iv) The plots are allocated to different size classes, for which separate analyses are made. Thus a plant density estimate is obtained from each size category of plots and these estimates are then combined through assigning to each estimate a weight inversely proportional to the variance of the corresponding estimator. Our plot size categories had 25% intervals, i.e. the plot size categories were 100%, 75-99%, 50-74%, and 25-49% of the nominal plot size; no plots were smaller than 25% of the nominal plot size. This method is denoted *CLASSWISE*.

(v) Regression analysis was applied, using a model specification where plot size is included as a predictor variable and plant density is a parameter that is estimated. This method is denoted *REGRESSION*.

In the following more details about the different methods are provided. While the methods *BASELINE* and *THRESHOLD* should be straightforward to understand from the previous short description, the other methods require further explanation.

The idea behind *RECALCULATION* is to change some plots from being registered as "absence" to being registered as "presence", with regard to the target species, if they are smaller than the nominal plot size. The reason is that a larger plot has greater probability for the species to be present. The probability that at least one plant of the target species occurs if a plot (with a size smaller than the nominal) is enlarged is $p = 1 - e^{-\lambda z}$, with the same notation as previously and with z being the missing area. In this case the density, λ, was estimated from the subset of plots which had the nominal plot size. Following this, a uniformly distributed random number between 0 and 1 was drawn and a plot registered as an "absence plot" was changed to a "presence plot" if the random number was smaller than p. The intuition is that a small “missing” area implies a low probability of change from absence to presence whereas a large “missing” area implies a greater probability of change.

With the *CLASSWISE* method the sample plots were allocated to separate size classes and separate calculation of plant density according to Eq. 2 was made for each class, assuming that the plot area corresponded to the size of plots at the midpoint of the class. In case fewer than 5 observations were assigned to a specific class that class was discarded from the analysis. Using categories with at least 5 observations a weighted average plant density was computed, where the weights were chosen inversely proportional to the estimated approximate variance of the density estimator. The approximate variance obtained through Taylor linearization is (Ståhl *et al.* 2017)

$$V(\hat{\lambda}) = \frac{p}{na^2(1-p)} = \frac{1-e^{-a\lambda}}{na^2 e^{-a\lambda}} \qquad (3)$$

and a variance estimator is obtained by inserting an estimated λ or p in Eq. 3, based on empirical data.

In the REGRESSION method, estimation of plant density, λ, is regarded as a generalized linear model (GLM) problem, where the response variable $Y_i = 1 - I_i$ and thus equals 0 if the species is present on plot i and 1 otherwise, and the predictor variable a_i is the size of the ith plot. A GLM is constructed around a linear predictor $\eta_i = \beta_0 + \beta_1 a_i$, and a link function g that describes the relationship between the mean, μ_i, of the response variable and the linear predictor is selected,

$$\eta_i = g(\mu_i);$$

see, e.g., Myers et al. (2002, Section 5.2). The expected response may now be written as $\mu_i = g^{-1}(\eta_i) = g^{-1}(\beta_0 + \beta_1 a_i)$, where g^{-1} is the inverse of the link function g. In the case of a homogeneous Poisson point process, the mean of Y_i is $\mu_i = e^{-\lambda a_i}$. If g is the natural logarithm function, $\beta_0 = 0$, and $\beta_1 = -\lambda$, then $g^{-1}(\beta_0 + \beta_1 a_i) = e^{-\lambda a_i}$. Thus, handling of different plot sizes can be treated as a GLM with a logarithmic link function, where plot size is included as a predictor variable and plant density is the model parameter to be estimated. By, e.g., Myers et al. (2002, Section 5.3), the estimator of the model parameter is found by solving the likelihood score equation, which in our setting can be expressed as

$$\sum_{i=1}^{n} \frac{(Y_i - e^{-\lambda a_i})a_i}{1 - e^{-\lambda a_i}} = 0. \qquad (4)$$

Let $\bar{Y}$ be the sample mean of $Y_1, \dots, Y_n$. If all plot sizes are equal to a, then the solution of the above equation can be written as $\hat{\lambda} = -a^{-1} \ln \bar{Y}$, i.e., it coincides with the estimator (2). If the plot sizes are not equally large, then there is no explicit solution to equation (4), but it can be solved numerically using standard software for GLMs. From a general expression for the asymptotic variance-covariance matrix of a GLM estimator in Myers et al. (2002, p. 166), it follows that the asymptotic variance of the GLM estimator $\hat{\lambda}$ can be written as

$$V(\hat{\lambda}) = \left(\sum_{i=1}^{n} \frac{a_i^2 e^{-\lambda a_i}}{1 - e^{-\lambda a_i}}\right)^{-1}. \qquad (5)$$

If all plot sizes equal a, then (5) coincides with (3).

We also address change estimation between two arbitrary time points, t_2 and t_1; the indices 2 and 1 are introduced to distinguish between the two time points. As in Ståhl *et al.* (2017) we assume the following: At time point 1, the locations of plants follow a homogeneous Poisson point process Λ_1 with density λ_1. In the time interval between t_1 and t_2, each existing plant from time point t_1 has probability π of surviving, independently of other plants, implying that the plants retained constitute a homogeneous Poisson process Λ_1^* with density $\lambda_1^* = \pi\lambda_1$ (see, e.g., Cressie 1991). At t_2, it is assumed that the locations of plants follow the superposition of two independent processes, Λ_1^* and Λ_2^*, where the latter is a homogeneous Poisson point process of newly regenerated plants with density λ_2^*. This implies that the locations of plants at time point t_2 follow a homogeneous Poisson point process Λ_2 with density $\lambda_2 = \lambda_1^* + \lambda_2^*$ (see, e.g., Cressie 1991). Let $\lambda_3 = (1-\pi)\lambda_1$. Ståhl *et al.* (2017) derived the following probabilities for an individual permanent plot of size a_i,

$$\pi_{00i} = P(\text{absence of plants at both time points}) = e^{-a_i(\lambda_2+\lambda_3)},$$
$$\pi_{11i} = P(\text{presence of plants at both time points}) = 1 - e^{-a_i\lambda_1} - e^{-a_i\lambda_2} + e^{-a_i(\lambda_2+\lambda_3)},$$
$$\pi_{01i} = P(\text{absence at time point 1 and presence at time point 2}) = e^{-a_i\lambda_1} - e^{-a_i(\lambda_2+\lambda_3)},$$
$$\pi_{10i} = P(\text{presence at time point 1 and absence at time point 2}) = e^{-a_i\lambda_2} - e^{-a_i(\lambda_2+\lambda_3)}.$$

Assume that we have presence-absence data from n permanent field plots of sizes a_i, $i = 1, \ldots, n$, i.e., each of the n sample plots from time point 1 are revisited at time point 2. Define I_{rsi}, where $r, s = 0, 1$, and $i = 1, \ldots, n$, such that for plot i: I_{00i} equals 1 if the species is absent at both time points and 0 otherwise; I_{11i} equals 1 if the species is present at both time points and 0 otherwise; I_{01i} equals 1 if the species is absent at t_1 and present at t_2; and $I_{10i} = 1 - I_{00i} - I_{11i} - I_{01i}$. We estimate $\boldsymbol{\lambda} = (\lambda_1, \lambda_2, \lambda_3)'$ using maximum likelihood (see, e.g., Rao 1973), i.e., the maximum likelihood estimator is any $\boldsymbol{\lambda} = (\lambda_1, \lambda_2, \lambda_3)'$ that maximizes the likelihood function

$$L(\boldsymbol{\lambda}) = \prod_{i=1}^{n} {\pi_{00i}}^{I_{00i}} {\pi_{11i}}^{I_{11i}} {\pi_{01i}}^{I_{01i}} {\pi_{10i}}^{I_{10i}}.$$

For *BASELINE*, *THRESHOLD*, and *RECALCULATION*, the plot sizes were set to the nominal size for all plots not discarded in the analysis. Due to the rather poor performance of method *CLASSWISE* we did not consider it for change estimation. For the *REGRESSION* method, a_i was always the actual size of the plot.

Sampling simulation

Sampling simulation was applied to evaluate the performance of the different methods for handling variable plot sizes in the artificial landscapes previously described. Circular sample plots with the nominal size 100 m^2 (corresponding to the large plot size in the Swedish NFI; Fridman *et al.* 2014) were allocated entirely at random across the study landscape. The sample size was always 500 plots, i.e. our intention was to mimic a survey with a fairly large sample size. On each of the sample plots a presence-absence assessment was conducted. If a plot was located at a stand boundary (cf. Fig 1) it was divided, and only the largest sub-plot was retained and used in the calculations.

The sampling simulations were conducted with 10,000 replications for each of the five methods and each of the cases (Cases I-III, with subcases) and in each replication plant density, λ, was estimated. For each subcase and method, we used the 10,000 estimates of λ for estimating bias, standard deviation (S.d.), and root mean square error (RMSE) of the plant density estimator.

It should be noted that the true value of the plant density may vary slightly from one artificial landscape to the next. Therefore, all values of bias, standard deviation, and RMSE are given as percentages of the true density. That is

$$\widehat{\mathrm{Bias}} = 100\frac{\widehat{\mathrm{Bias}}(\hat{\lambda})}{\lambda}, \qquad \widehat{\mathrm{S.d.}} = 100\frac{\widehat{\mathrm{S.d.}}(\hat{\lambda})}{\lambda}, \qquad \text{and} \qquad \widehat{\mathrm{RMSE}} = 100\frac{\widehat{\mathrm{RMSE}}(\hat{\lambda})}{\lambda},$$

where $\hat{\lambda}$ denotes estimated plant density (for a specific subcase and method). All computations were made using the software R (R Core Team 2018)

Calculations based on the National Forest Inventory data

Using the National Forest Inventory data we computed state and change densities for each of the five methods by region and species. In this case no true densities were available and this part of the study only focused on assessing differences in numerical values between the different methods. The computations were made, following the previously described estimators for the five different methods, using the software R (R Core Team 2018). The dataset reference is Ståhl *et al.* (2019).

Results

Sampling simulations

In Figure 4, the bias of the estimators corresponding to the different methods are presented for the populations with small stands (50% divided plots). In Figures 5 and 6 the corresponding results for intermediate and large stands, respectively, are presented (25% and 10% divided plots).

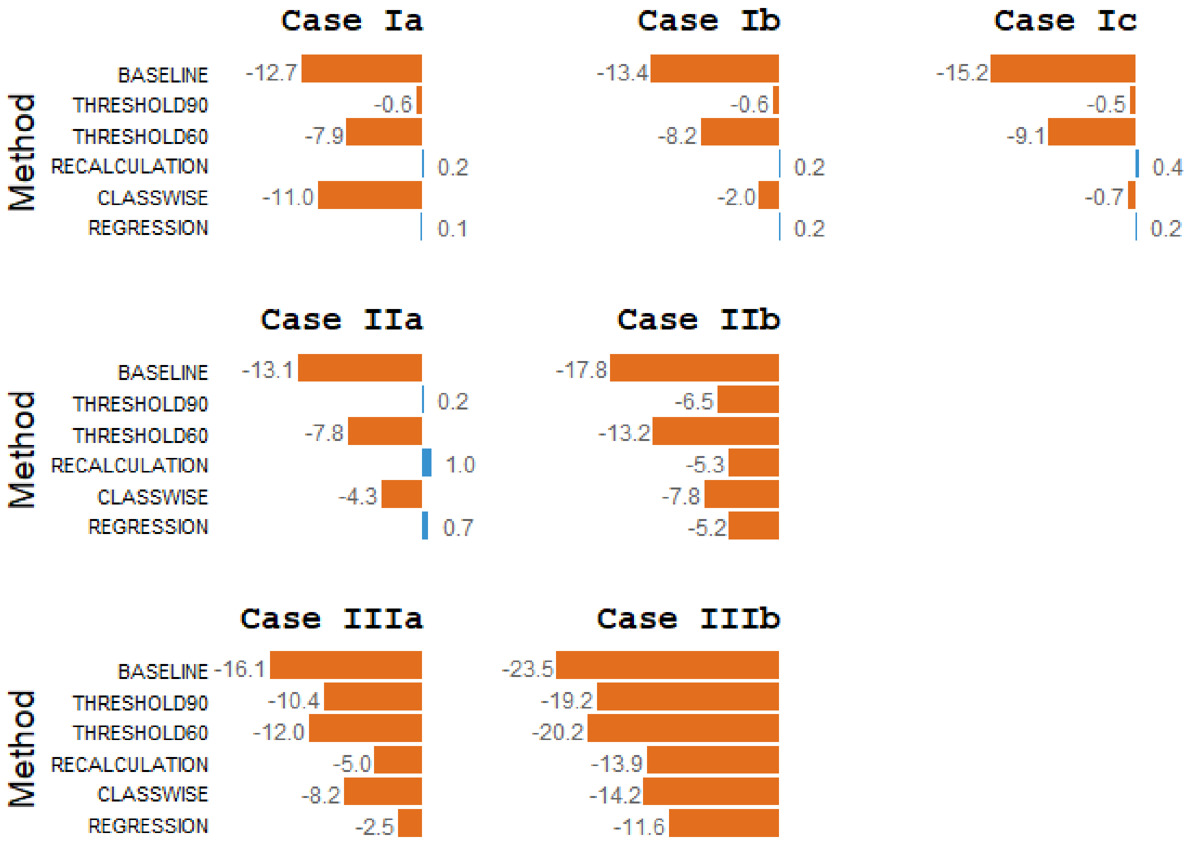

Figure 4. Bias (%) of the density estimators in the case of small stands (50% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Figure 5. Bias (%) of the density estimators in the case of intermediate stands (25% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

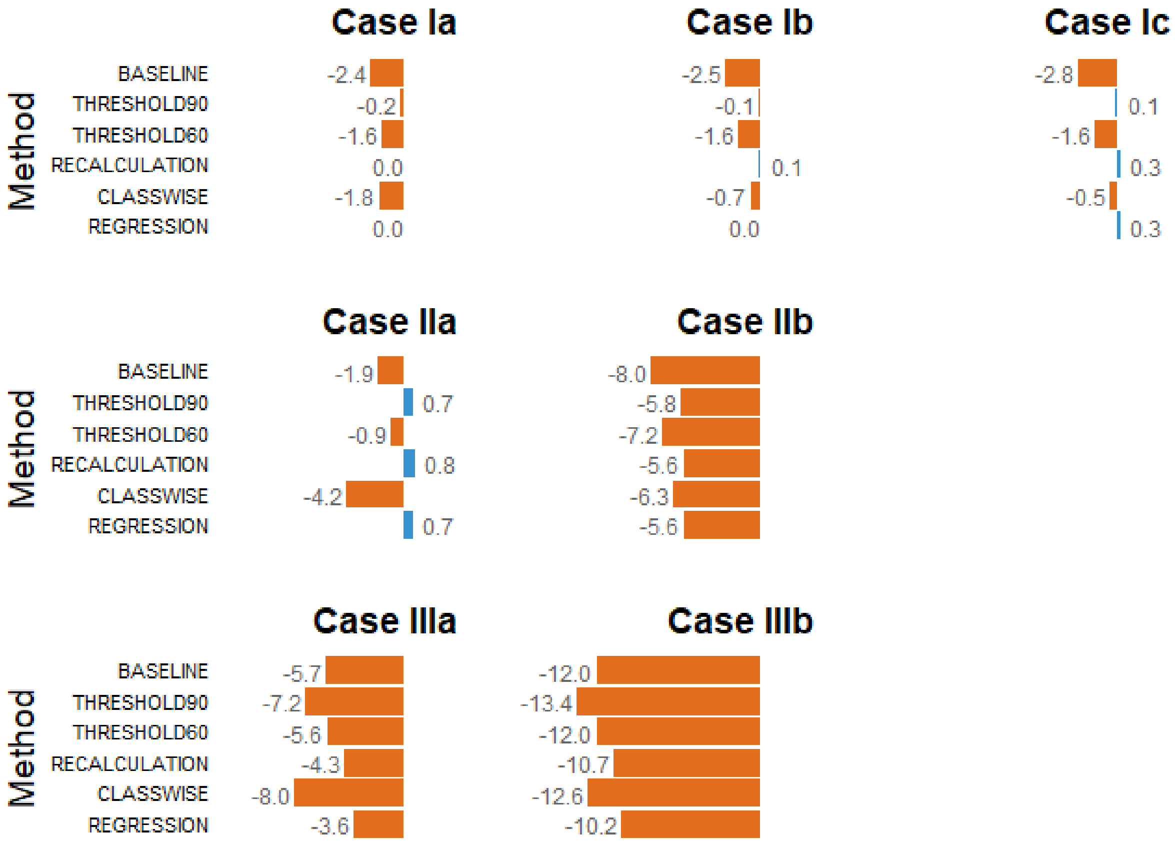

Figure 6. Bias (%) of the density estimators in the case of large stands (10% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

The BASELINE method often resulted in fairly large bias. THRESHOLD90 in most cases lead to an improvement whereas THRESHOLD60 typically resulted in larger bias than THRESHOLD90. The RECALCULATION method consistently was among the methods leading to the smallest absolute bias whereas the CLASSWISE method led to large bias in most cases.

Overall, the REGRESSION method performed best (in terms of small absolute bias). The second best method was RECALCULATION and the third best THRESHOLD90.

Studying the different methods across different artificial landscapes, the most difficult cases (i.e. the ones where large bias occurred) were the landscapes where the population densities varied between different strata, and no information was available to handle stratum membership in the estimation (Cases IIb and IIIb). The cases with higher densities along stand boundaries (Cases IIIa and IIIb) also led to severely biased estimators. In case stratum membership indicators were available and the densities were even within the stands (Case IIa), varying densities between strata did not, however, incur severe bias.

Full results for bias, standard deviation, and root mean square error (RMSE) are given in Appendix A. No major differences in standard deviations were obtained for the different methods, exept for CLASSWISE which typically resulted in larger standard deviations of the estimators compared to the other methods.

Turning to change estimation, below we present results for a case where the population densities at time point two were 40% larger than at time point one. Similar results were obtained when the change was 15%; results for the latter case are presented in Appendix B.

In Figures 7, 8 and 9 change estimation results are shown for small, intermediate, and large stands, respectively.

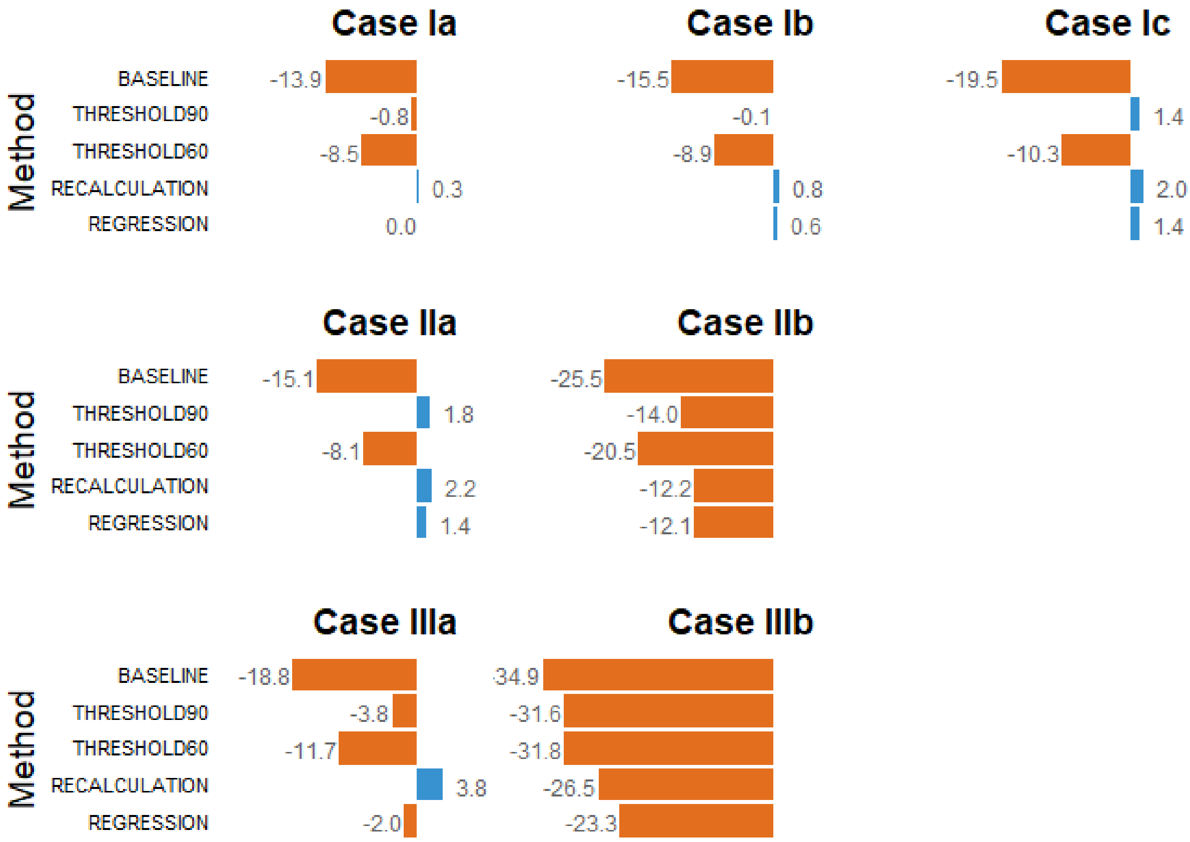

Figure 7. Bias (%) of the estimators of change in the case of small stands and $\lambda_2 = 1.4\lambda_1$*, i.e. the density at time point two was 40% higher than the density at time point 1. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

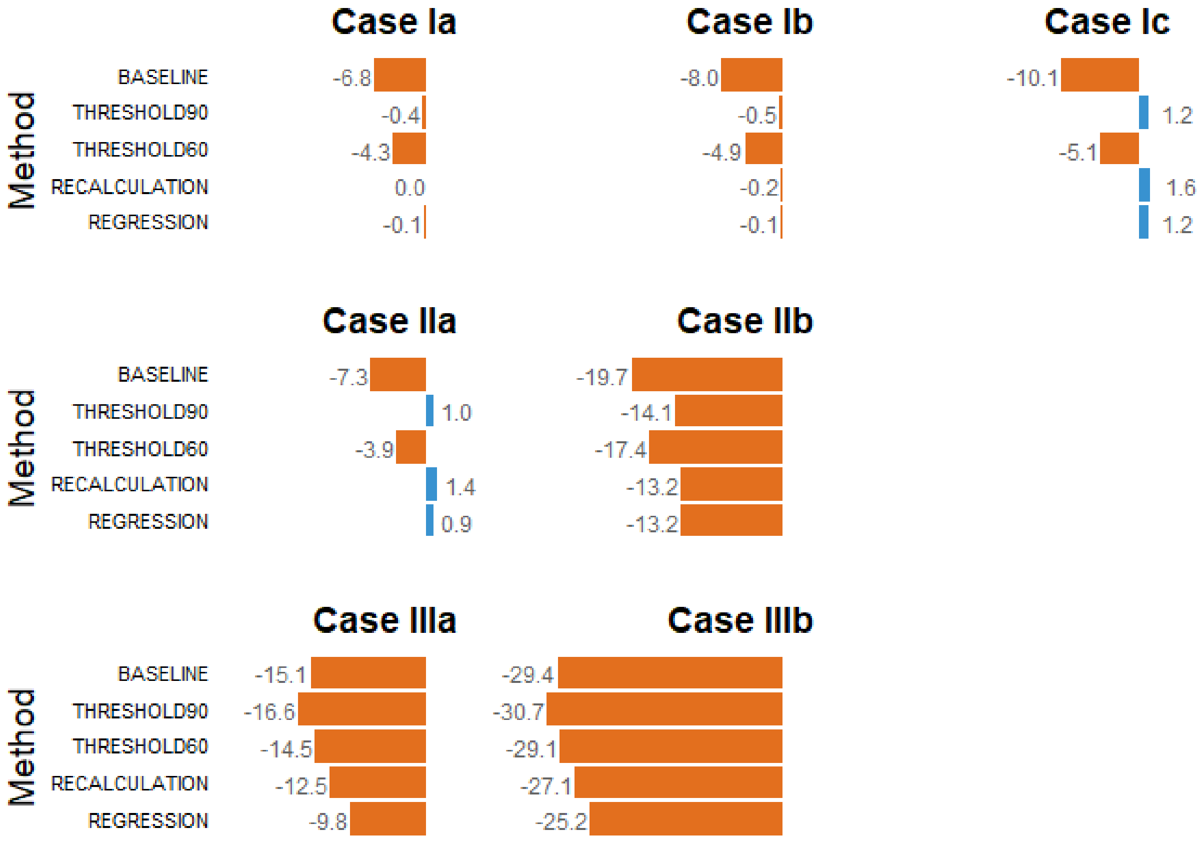

Figure 8. Bias (%) of the estimators of change in the case of intermediate stands and $\lambda_2 = 1.4\lambda_1$*, i.e. the density at time point two was 40% higher than the density at time point 1. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

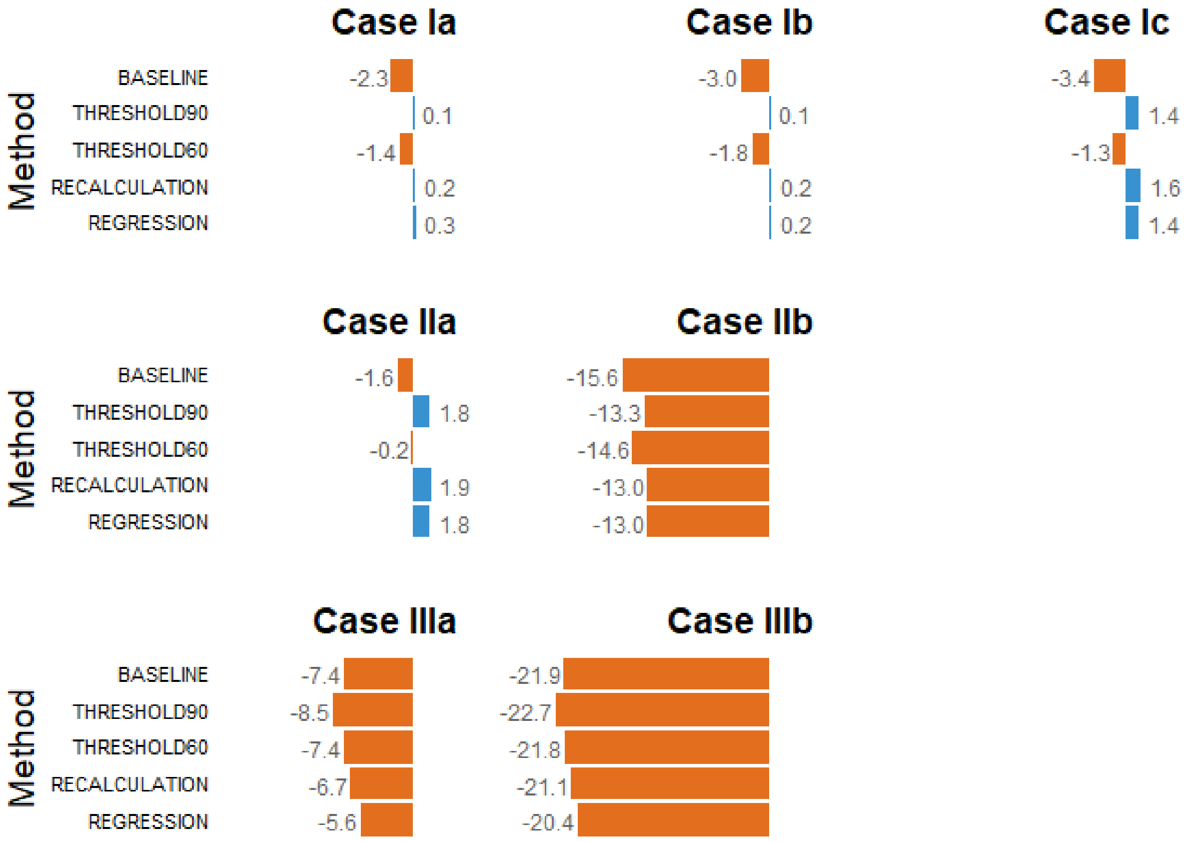

Figure 9. Bias (%) of the estimators of change in the case of large stands and $\lambda_2 = 1.4\lambda_1$*, i.e. the density at time point two was 40% higher than the density at time point 1. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

The change estimation results turned out to be similar to the state estimation results. The regression method performed best, mostly followed by RECALCULATION and THRESHOLD90. When densities varied between strata and stratum membership was not known, large biases were obtained.

The numerical results based on NFI data are presented in Tables 2 and 3, for *Trientalis europaea* (L.) and *Melampyrum pretense* (L.), for two different NFI regions (cf. Fig 3).

Table 2. Density estimates (plants per 100 m^2) for Trientalis europaea (L.) based on NFI data

Method	*Region 2*	*Region 4*
BASELINE	0.802	0.578
THRESHOLD.90	0.811	0.584
THRESHOLD.60	0.809	0.582
RECALCULATION	0.837	0.618
CLASSWISE	0.827	0.614
REGRESSION	0.836	0.618

Table 3. Density estimates (plants per 100 m^2) for Melampyrum pratense (L.) based on NFI data

Method	*Region 2*	*Region 4*
BASELINE	0.934	0.500
THRESHOLD.90	0.940	0.505
THRESHOLD.60	0.948	0.506
RECALCULATION	0.956	0.525
CLASSWISE	0.962	0.519
REGRESSION	0.974	0.532

The differences in results between the methods appear to be in the same order of magnitude as those obtained from the simulation studies in artificial populations. The regression method consistently resulted in the highest density estimates.

Discussion

In statistically sound sample surveys of forests or landscapes the sampling units should be selected randomly in order to ensure unbiased estimators of the studied population parameters (e.g. Gregoire and Valentine 2008). Important examples of such surveys are the national forest inventories that are being conducted in a large number of countries worldwide (Tomppo *et al.* 2010). When sample plots are randomly allocated in the landscape some will fall across boundaries between different land use or land cover categories. In such cases plots are often divided, since results are normally required to be presented separately by different land use or land cover categories. Intuitive approaches, such as purposively moving plots away from boundaries in order to avoid plot divisions typically lead to biased estimates since conditions at edges differ from interior conditions (Harper et al., 2005; Esseen *et al.* 2016). Several methods have been developed for coping with boundary plots in monitoring programmes. For some types of variables bias incurred by plot boundary issues can be avoided by applying special field protocols for such plots (e.g. Ducey et al. 2001), where features, such as trees, on plots are double counted on parts of a plot located close to a boundary. Alternatively, estimators that take subplot size into account can be applied (e.g. Fridman *et al.* 2014). However, none of these opportunities are available for presence-absence registrations and thus there is currently a gap in the methodological tool-kit available for analyzing data from forest and landscape surveys. The current study offers methods to fill this gap.

In this study we assume that plots at boundaries are divided and presence-absence registrations are only conducted on the larger subplot. Other reasons for variable plot size exist as well, such as accounting for disturbances on plots (e.g. large rocks) during the calculations or when merging data from several surveys into a single analysis (e.g. Grafström *et al.*, 2019).

Studying the simulation results for state estimation it is clear that the *BASELINE* method, i.e. treating the plots as if they all had the nominal size, leads to considerable negative bias, especially in the case of a high proportion divided plots. For example, with 25% of the plots being divided the density was underestimated by about 5 to 18%. However, with a small proportion of divided plots (<10%) the bias of the BASELINE method was mostly moderate. The baseline method also consistently resulted in the lowest density estimates based on the empirical NFI data.

The *THRESHOLD* method can be seen as a straightforward modification of the *BASELINE* method, in which all plots smaller than a certain proportion of the nominal size are discarded. When a 90% size threshold was used (i.e. all plots smaller than 90% of the nominal size were discarded), substantial improvements in terms of reduced bias were obtained in most simulated populations, although at the expense of a slightly increased standard deviation due to a smaller number of plots available for the density estimation. With a 60% size threshold (i.e. all plots smaller than 60% of the nominal size were discarded) the bias was larger, which indicates that the size threshold should probably not deviate too far from 100% when this method is applied. However, the results from empirical data were somewhat inconclusive as *THRESHOLD90* sometimes resulted in lower density estimates than *THRESHOLD60*. Overall, the *THRESHOLD* method can be recommended in case a simple and straightforward approach to handling the problem of variable plot sizes is required. It is also a straightforward adjustment method for cases when frequencies are not transformed to plant density estimates. However, it should be noted that the THRESHOLD method is prone to substantial bias in case plant densities close to patch boundaries differ from interior densities. This was manifested by large negative biases when the *THRESHOLD* method was used in our simulated Case III populations. The reason is that plots at patch boundaries would often be discarded due to being divided and such plots (in the Case III populations) normally had higher plant densities. Thus, this method should be used with caution in case it can be expected that interior and boundary conditions differ with regard to plant density.

The *RECALCULATION* method in most cases led to good results in the simulation, mostly somewhat better than the *THRESHOLD* method in terms of absolute bias. Based on empirical data it typically resulted in slightly larger values than the *THRESHOLD* method. Thus, the *RECALCULATION* method can also be recommended in applications, although it is slightly more complicated to apply compared to the

THRESHOLD method. It would also be a good alternative to the THRESHOLD method in cases when frequencies are not transformed to densities.

The *CLASSWISE* method performed somewhat worse than the *THRESHOLD* and *RECALCULATION* methods. The reason is probably the weighting procedure involved, which requires variance estimates to be computed for the density estimates from the different classes. It is known from other studies (Grafström *et al.* 2019) that estimators and their corresponding variance estimators are correlated, a phenomenon that might have added to the bias in this study. To avoid this type of additional bias, the sample size in each class must be large, which is a restriction in applications and the method cannot be recommended in the case of surveys with small sample sizes. Moreover, the standard deviation of estimates based on the *CLASSWISE* method was high compared to the other methods.

Although theoretically more complicated than the other methods, the *REGRESSION* method typically led to the best results in the simulations in terms of avoiding bias in the density estimators. Standard deviations of the REGRESSION method normally were comparable to the best of the other methods. It also consistently lead to the largest density estimates based on empirical data. An advantage of this method is that it has a strict theoretical foundation (e.g. Myers *et al*. 2002). Further, the application of REGRESSION is simplified by straightforward access to statistical software, where the proposed GLM regression technique (Nelder and Baker 1972) is implemented.

Thus, the *REGRESSION* method is our preferred choice for density estimation using data with variable plot sizes, at least in case the analyst is willing to invest some additional time in the analysis. Our second best choice is the RECALCULATION method, which requires little additional complication during the analyses. Our third best method, *THRESHOLD,* can be applied at very minimal additional burden during the analysis.

The study revealed the importance of having access to stratum information when plant population densities vary among strata, which is typically the case (*e.g.*, Roberts and Gilliam 1995). Comparisons in this regard involved the Case *IIa* population *vs* the Case *IIb* population, and the Case *IIIa vs* the Case *IIIb* populations. In the *a*-cases, stratum identifiers were assumed to be available and could be utilized in the estimators, i.e. stratum level estimates were first computed and then aggregated to estimates for the entire study area. In the *b*-cases stratum identifiers were not available. For those cases, all methods performed rather poorly, in terms of negative bias. The reason for the negative bias is the non-linear estimator (Eq. 2). In contrast, many of the methods worked well when stratum identifiers were available. We suggest that using stratified approaches to density estimation based on presence-absence data is an interesting area for further study. Stratification may be based on land use or land cover categories, or more advanced schemes employing several sources of information available wall-to-wall for the study area (*e.g.* Saarela *et al.* 2015). Further, an interesting development of the *REGRESSION* method would be to include such information as additional predictor variables.

The results from the change estimation study followed the general patterns obtained from the state estimation study. Substantial bias of the change estimators were obtained for several methods, especially if stratum membership was not known. Varying the level of change (from 40% to 15%) did not lead to any major changes in the result patterns.

The motivation for including the Case III artificial populations was to generically study complicated cases with dependencies between plant density and plot size. As expected, it was difficult to find an efficient method to handle variable plot size in this case. While we could have evaluated alternative cases with decreased densities along stand boundaries as well, our intention was, however, to generically address this type of problem rather than numerically evaluating a large number of different alternatives.

It should be noted that our methods and results are based on the assumption that plants are located according to a Poisson process (e.g. Greig-Smith 1983; Bonham 2013). While this may only occasionally be the case in real life, this model assumption still is often used in studies of this kind (ibid.) due to the lack of straightforward alternatives. The Poisson process is an important reference model for modelling plant occurrences (e.g. Bonham 2013), but is not useful for modelling, e.g., clustered patterns of plant occurrences (e.g. Hwang & He 2011). In a parallel study (Ekström *et al.* 2019), we develop new theory for linking presence-absence data with plant density under spatial cluster models of Neyman-Scott type.

Special caution is needed when applying the methods proposed in this study to common species inventoried in large plots or uncommon species inventoried in small plots. As described in Ståhl *et al.* (2017) different real plant densities imply different optimal plot sizes, and when the plot sizes deviate largely from the optimal plot size the density estimates are very uncertain. This was the reason for our choice of plant densities in the simulation study.

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Data availability

The dataset from the Swedish National Forest Inventory (for the specific species, years, and regions used in the study) is deposited in the Dryad repository: https://doi.org/10.5061/dryad.nvx0k6dn1

The full dataset from the Swedish National Forest Inventory is available upon request from the Swedish University of Agricultural Sciences (https://www.slu.se/riksskogstaxeringen).

Author contributions

GS conceived the idea and developed the methods together with ME. GS and ME jointly wrote a draft version of the manuscript. ME performed the statistical analyses. P-AE and BGJ contributed with ecological knowledge. JD provided empirical data and contributed with knowledge from practical surveys. AG contributed with statistical knowledge. All authors contributed to the writing of the first complete version of the manuscript and to the revision of the manuscript.

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APPENDIX A: Detailed state estimation results

In Tables A1, A2 and A3 detailed results from the state estimation simulations are provided in terms of bias, standard deviation and root mean square error. (Since the tables are large they are presented on separate pages.)

Table A1. *Bias (%), standard deviation (S.d. %), and RMSE (%) of the density estimators in the case of small stands (50% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

Case	Subcase		Method					
			BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*CLASSWISE*	*REGRESSION*
I	(a)	$\widehat{\text{Bias}}$	-12.68	-0.62	-7.87	0.18	-11.01	0.14
		$\widehat{\text{S.d.}}$	6.65	9.03	7.24	8.19	31.09	7.63
		$\widehat{\text{RMSE}}$	14.32	9.05	10.69	8.19	32.98	7.63
	(b)	$\widehat{\text{Bias}}$	-13.40	-0.60	-8.19	0.22	-1.99	0.20
		$\widehat{\text{S.d.}}$	5.24	7.30	5.79	6.61	13.59	6.08
		$\widehat{\text{RMSE}}$	14.39	7.33	10.03	6.61	13.74	6.08
	(c)	$\widehat{\text{Bias}}$	-15.16	-0.47	-9.06	0.36	-0.68	0.17
		$\widehat{\text{S.d.}}$	4.73	7.20	5.40	6.48	6.12	5.68
		$\widehat{\text{RMSE}}$	15.88	7.22	10.55	6.49	6.16	5.68
II	(a)	$\widehat{\text{Bias}}$	-13.11	0.19	-7.78	1.02	-4.33	0.70
		$\widehat{\text{S.d.}}$	5.68	8.02	6.35	7.33	9.17	6.64
		$\widehat{\text{RMSE}}$	14.29	8.03	10.04	7.40	10.14	6.67
	(b)	$\widehat{\text{Bias}}$	-17.83	-6.47	-13.21	-5.27	-7.75	-5.16
		$\widehat{\text{S.d.}}$	5.02	6.95	5.56	6.33	14.56	5.82
		$\widehat{\text{RMSE}}$	18.53	9.50	14.34	8.24	16.50	7.78
III	(a)	$\widehat{\text{Bias}}$	-16.13	-10.40	-11.96	-4.95*	-8.24	-2.48
		$\widehat{\text{S.d.}}$	5.17	7.14	5.79	6.64*	6.86	6.20
		$\widehat{\text{RMSE}}$	16.93	12.61	13.29	8.28*	10.72	6.68
	(b)	$\widehat{\text{Bias}}$	-23.49	-19.19	-20.24	-13.90	-14.23	-11.63
		$\widehat{\text{S.d.}}$	4.17	5.59	4.60	5.19	5.62	4.92
		$\widehat{\text{RMSE}}$	23.85	19.99	20.76	14.84	15.30	12.63

* Value computed without one replicate that gave $\hat{\lambda} = \infty$.

Table A2. *Bias (%), standard deviation (S.d. %), and RMSE (%) of the density estimators in the case of intermediate stands (25% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

Case	Subcase		Method					
			BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*CLASSWISE*	*REGRESSION*
I	(a)	$\widehat{\text{Bias}}$	-5.85	-0.08	-3.67	0.24	-4.44	0.24
		$\widehat{\text{S.d.}}$	6.97	7.98	7.24	7.65	20.42	7.42
		$\widehat{\text{RMSE}}$	9.10	7.98	8.12	7.66	20.89	7.43
	(b)	$\widehat{\text{Bias}}$	-6.49	-0.27	-4.05	0.10	-1.82	0.07
		$\widehat{\text{S.d.}}$	5.61	6.42	5.83	6.21	13.05	6.01
		$\widehat{\text{RMSE}}$	8.58	6.43	7.10	6.21	13.17	6.01
	(c)	$\widehat{\text{Bias}}$	-7.34	-0.05	-4.31	0.36	-0.43	0.28
		$\widehat{\text{S.d.}}$	5.20	6.28	5.54	6.04	6.21	5.70
		$\widehat{\text{RMSE}}$	9.00	6.28	7.02	6.05	6.22	5.71
II	(a)	$\widehat{\text{Bias}}$	-5.91	0.61	-3.39	0.91	-2.89	0.79
		$\widehat{\text{S.d.}}$	5.99	7.04	6.30	6.75	7.21	6.46
		$\widehat{\text{RMSE}}$	8.42	7.07	7.15	6.81	7.76	6.50
	(b)	$\widehat{\text{Bias}}$	-11.50	-5.97	-9.34	-5.45	-7.23	-5.42
		$\widehat{\text{S.d.}}$	5.25	6.10	5.49	5.85	12.41	5.63
		$\widehat{\text{RMSE}}$	12.64	8.54	10.84	7.99	14.36	7.81
III	(a)	$\widehat{\text{Bias}}$	-11.30	-12.74	-10.55	-7.42	-11.87	-5.76
		$\widehat{\text{S.d.}}$	5.44	5.91	5.62	5.87	5.96	5.87
		$\widehat{\text{RMSE}}$	12.54	14.05	11.96	9.46	13.28	8.22
	(b)	$\widehat{\text{Bias}}$	-17.91	-19.22	-17.29	-14.21	-16.92	-12.88
		$\widehat{\text{S.d.}}$	4.51	4.95	4.67	4.89	6.36	4.84
		$\widehat{\text{RMSE}}$	18.47	19.85	17.91	15.03	18.08	13.76

Table A3. *Bias (%), standard deviation (S.d. %), and RMSE (%) of the density estimators in the case of large stands (10% divided plots). In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

Case	Subcase		Method					
			BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*CLASSWISE*	*REGRESSION*
I	(a)	$\widehat{\mathrm{Bias}}$	-2.40	-0.21	-1.58	-0.03	-1.75	-0.05
		$\widehat{\mathrm{S.d.}}$	6.99	7.36	7.09	7.26	10.35	7.16
		$\widehat{\mathrm{RMSE}}$	7.39	7.36	7.26	7.26	10.50	7.16
	(b)	$\widehat{\mathrm{Bias}}$	-2.50	-0.06	-1.58	0.06	-0.66	0.05
		$\widehat{\mathrm{S.d.}}$	5.71	6.06	5.80	5.95	6.02	5.87
		$\widehat{\mathrm{RMSE}}$	6.23	6.06	6.02	5.95	6.05	5.87
	(c)	$\widehat{\mathrm{Bias}}$	-2.77	0.13	-1.60	0.27	-0.47	0.26
		$\widehat{\mathrm{S.d.}}$	5.52	5.92	5.64	5.85	5.71	5.71
		$\widehat{\mathrm{RMSE}}$	6.17	5.92	5.86	5.86	5.73	5.72
II	(a)	$\widehat{\mathrm{Bias}}$	-1.88	0.66	-0.92	0.79	-4.24	0.74
		$\widehat{\mathrm{S.d.}}$	6.20	6.57	6.30	6.49	9.38	6.38
		$\widehat{\mathrm{RMSE}}$	6.48	6.60	6.36	6.53	10.30	6.42
	(b)	$\widehat{\mathrm{Bias}}$	-7.97	-5.82	-7.15	-5.60	-6.30	-5.61
		$\widehat{\mathrm{S.d.}}$	5.37	5.67	5.45	5.62	5.69	5.52
		$\widehat{\mathrm{RMSE}}$	9.61	8.12	8.99	7.93	8.48	7.87
III	(a)	$\widehat{\mathrm{Bias}}$	-5.65	-7.16	-5.62	-4.29	-7.99	-3.62
		$\widehat{\mathrm{S.d.}}$	5.87	6.02	5.93	6.04	6.31	6.05
		$\widehat{\mathrm{RMSE}}$	8.15	9.35	8.17	7.41	10.18	7.05
	(b)	$\widehat{\mathrm{Bias}}$	-12.02	-13.39	-12.00	-10.68	-12.63	-10.15
		$\widehat{\mathrm{S.d.}}$	5.02	5.15	5.06	5.17	5.21	5.16
		$\widehat{\mathrm{RMSE}}$	13.03	14.34	13.02	11.87	13.66	11.38

Appendix B. Detailed change estimation results

In Figures B1, B2, and B3 change estimation results are presented for the case where the population change in density between period 1 and period 2 was 15%.

In Tables B1-B6, detailed results from the change estimation simulations are presented.

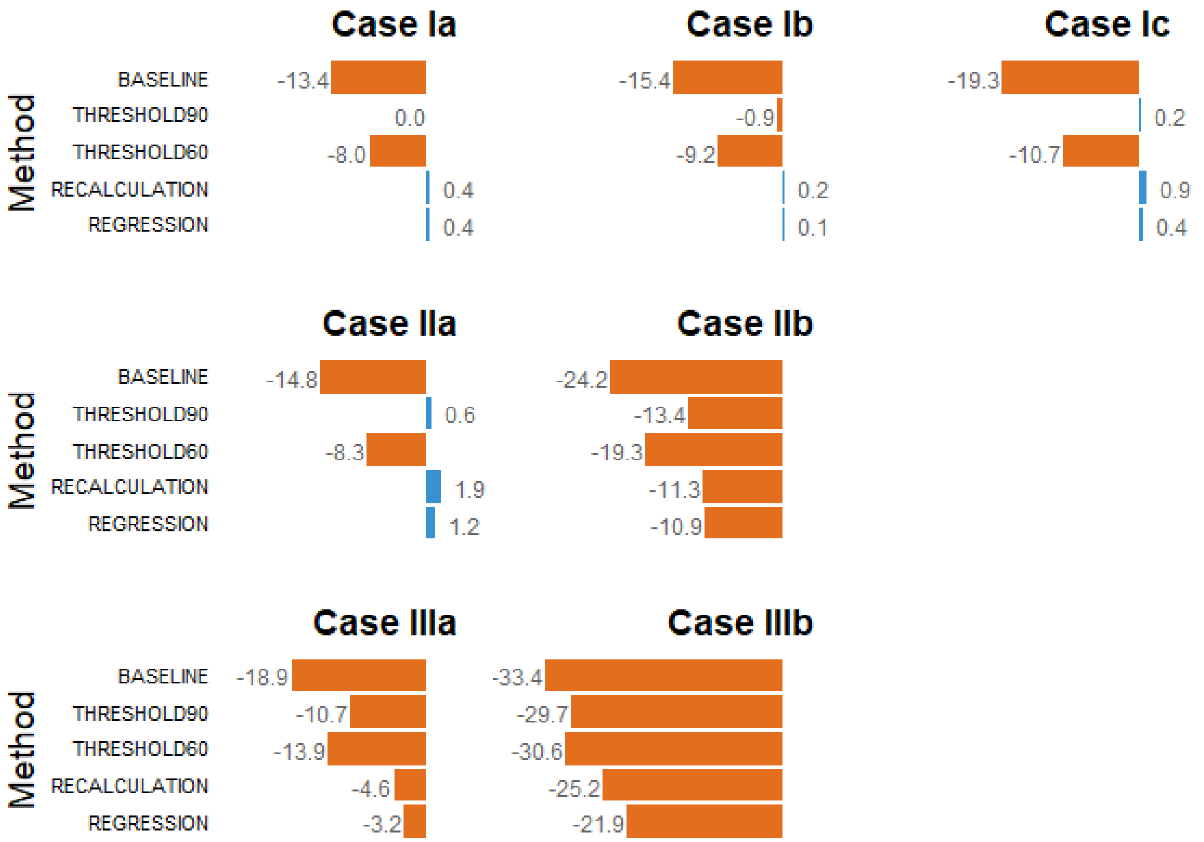

Figure B1. Bias (%) of the estimators of change in the case of small stands and $\lambda_2 = 1.15\lambda_1$*. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

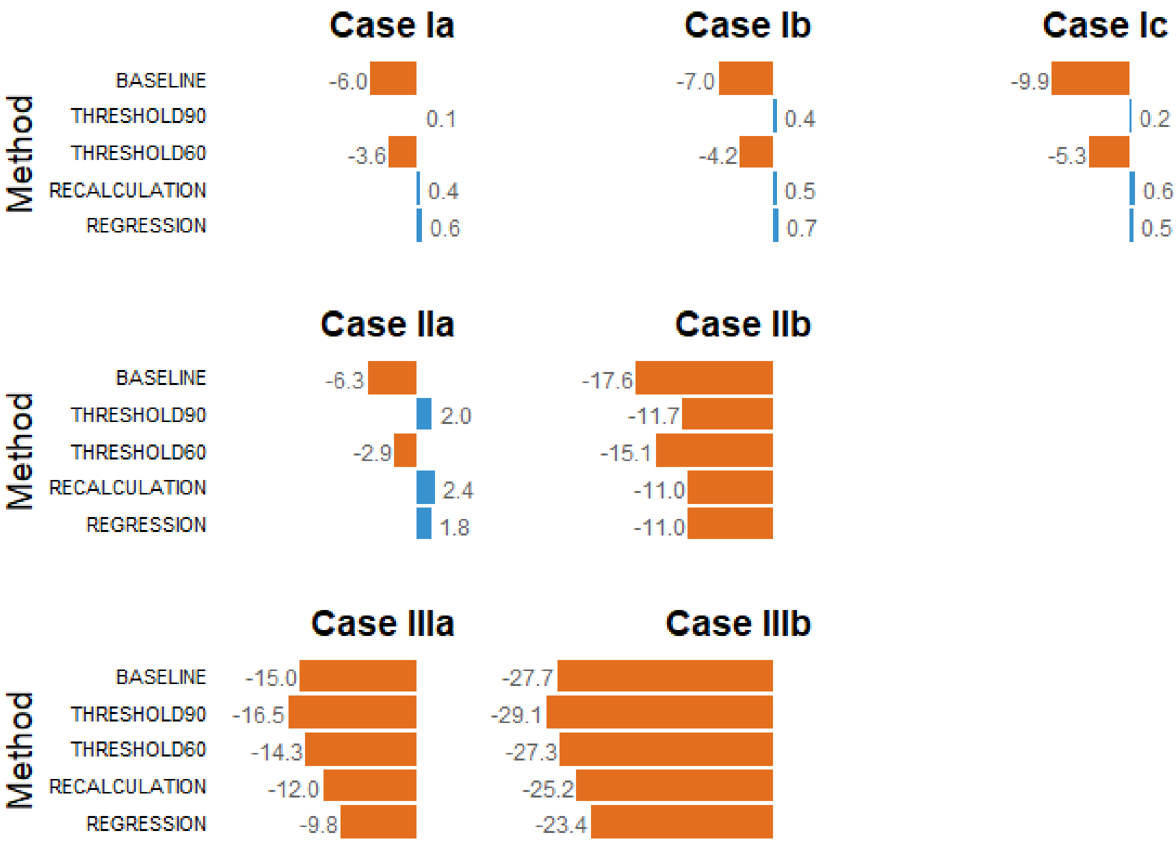

Figure B2. Bias (%) of the estimators of change in the case of intermediate stands and $\lambda_2 = 1.15\lambda_1$. *In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

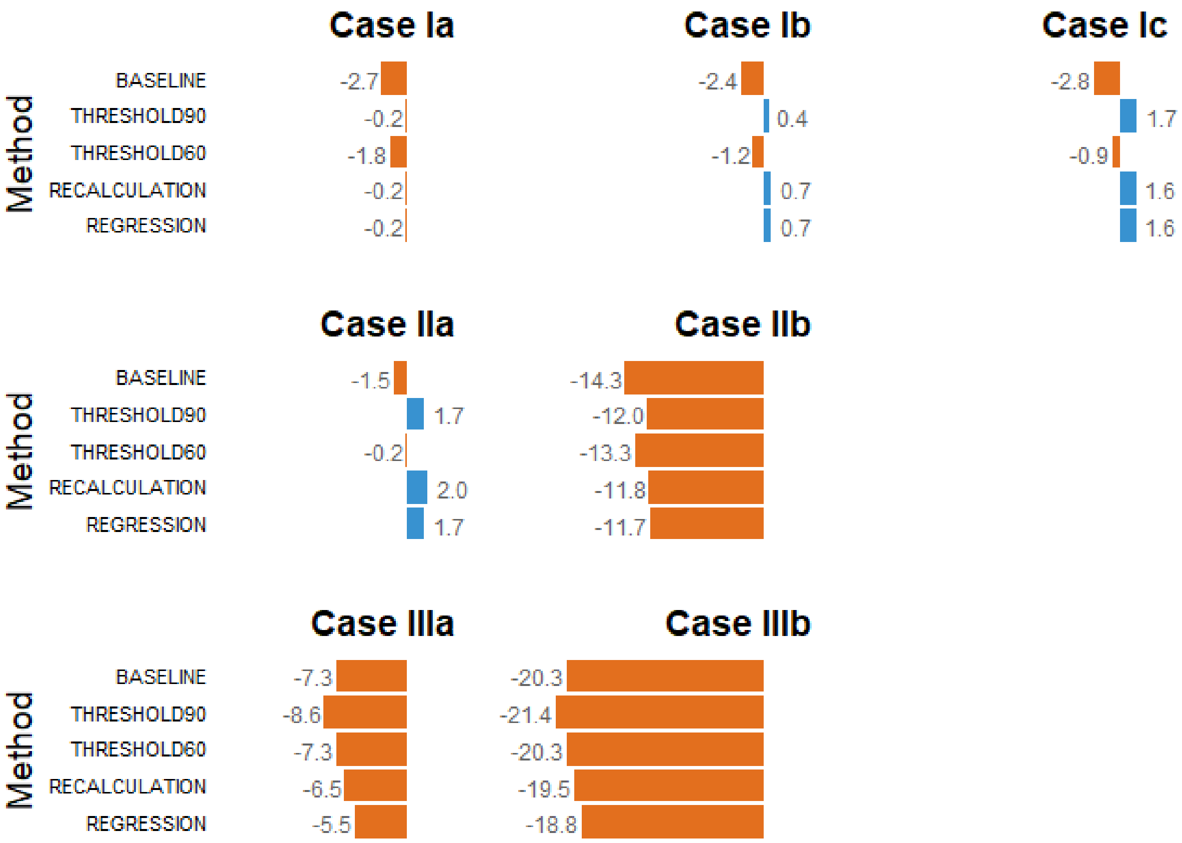

Figure B3. Bias (%) of the estimators of change in the case of large stands and $\lambda_2 = 1.15\lambda_1$. *In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.*

Table B1. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of small stands (50% divided plots). Here, $\lambda_2 = 1.15\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-12.77	-0.84	-8.03	0.09	0.02
			$\widehat{\text{S.d.}}$	6.72	9.17	7.38	8.32	7.72
			$\widehat{\text{RMSE}}$	14.43	9.21	10.91	8.32	7.72
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-12.85	-0.73	-8.02	0.13	0.07
			$\widehat{\text{S.d.}}$	6.39	8.74	7.06	7.87	7.37
			$\widehat{\text{RMSE}}$	14.35	8.77	10.69	7.87	7.37
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.38	-0.01	-7.96	0.40	0.37
			$\widehat{\text{S.d.}}$	50.87	70.02	56.37	64.82	58.96
			$\widehat{\text{RMSE}}$	52.60	70.01	56.93	64.82	58.95
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.39	-0.67	-8.24	0.22	0.20
			$\widehat{\text{S.d.}}$	5.40	7.59	5.96	6.83	6.28
			$\widehat{\text{RMSE}}$	14.44	7.62	10.17	6.83	6.29
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-13.65	-0.69	-8.36	0.22	0.19
			$\widehat{\text{S.d.}}$	5.19	7.33	5.78	6.59	6.08
			$\widehat{\text{RMSE}}$	14.61	7.37	10.16	6.60	6.08
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.38	-0.87	-9.19	0.22	0.09
			$\widehat{\text{S.d.}}$	42.56	61.99	48.09	56.16	50.36
			$\widehat{\text{RMSE}}$	45.25	62.00	48.96	56.16	50.36
	(c)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.04	-0.49	-8.94	0.47	0.30
			$\widehat{\text{S.d.}}$	4.86	7.20	5.51	6.60	5.81
			$\widehat{\text{RMSE}}$	15.80	7.22	10.50	6.61	5.81
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-15.59	-0.40	-9.17	0.53	0.31
			$\widehat{\text{S.d.}}$	4.86	7.36	5.54	6.74	5.86
			$\widehat{\text{RMSE}}$	16.33	7.37	10.71	6.76	5.87
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-19.26	0.21	-10.69	0.92	0.36
			$\widehat{\text{S.d.}}$	41.46	65.41	48.64	61.12	51.34
			$\widehat{\text{RMSE}}$	45.71	65.41	49.79	61.13	51.34
II	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.02	0.48	-7.63	1.19	0.82
			$\widehat{\text{S.d.}}$	5.70	8.13	6.34	7.34	6.65
			$\widehat{\text{RMSE}}$	14.21	8.14	9.92	7.44	6.70
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-13.25	0.50	-7.73	1.29	0.86
			$\widehat{\text{S.d.}}$	5.46	7.96	6.15	7.16	6.43

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\text{RMSE}}$	14.33	7.97	9.87	7.28	6.48
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-14.81	0.61	-8.34	1.94	1.18
			$\widehat{\text{S.d.}}$	45.48	67.09	51.72	62.70	54.21
			$\widehat{\text{RMSE}}$	47.83	67.09	52.39	62.73	54.22
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-17.78	-6.30	-13.12	-5.14	-5.08
			$\widehat{\text{S.d.}}$	5.08	7.06	5.61	6.45	5.89
			$\widehat{\text{RMSE}}$	18.49	9.46	14.27	8.25	7.78
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-18.61	-7.22	-13.93	-5.94	-5.84
			$\widehat{\text{S.d.}}$	4.78	6.71	5.31	6.04	5.56
			$\widehat{\text{RMSE}}$	19.22	9.86	14.91	8.47	8.06
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-24.20	-13.37	-19.34	-11.28	-10.90
			$\widehat{\text{S.d.}}$	39.35	55.55	43.99	52.62	46.27
			$\widehat{\text{RMSE}}$	46.19	57.13	48.05	53.82	47.54
III	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.98	-10.14	-11.76	-4.64	-2.48
			$\widehat{\text{S.d.}}$	5.25	7.94	5.96	7.93	6.28
			$\widehat{\text{RMSE}}$	16.82	12.88	13.19	9.19	6.76
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-16.37	-10.22	-12.04	-4.63	-2.57
			$\widehat{\text{S.d.}}$	5.37	9.62	6.10	11.26	6.51
			$\widehat{\text{RMSE}}$	17.23	14.03	13.50	12.18	7.00
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-18.94	-10.74	-13.90	-4.56	-3.18
			$\widehat{\text{S.d.}}$	45.75	82.40	52.73	94.74	55.24
			$\widehat{\text{RMSE}}$	49.51	83.10	54.52	94.84	55.33
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-23.39	-19.02	-20.09	-13.73	-11.64
			$\widehat{\text{S.d.}}$	4.20	5.63	4.68	5.24	4.93
			$\widehat{\text{RMSE}}$	23.76	19.83	20.63	14.70	12.64
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-24.69	-20.42	-21.46	-15.22	-12.97
			$\widehat{\text{S.d.}}$	4.14	5.53	4.56	5.18	4.86
			$\widehat{\text{RMSE}}$	25.04	21.15	21.94	16.08	13.85
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-33.39	-29.74	-30.64	-25.17	-21.86
			$\widehat{\text{S.d.}}$	34.44	45.92	38.31	44.37	40.42
			$\widehat{\text{RMSE}}$	47.97	54.70	49.06	51.01	45.95

Table B2. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of intermediate stands (25% divided plots). Here, $\lambda_2 = 1.15\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.98	-0.25	-3.81	0.11	0.09
			$\widehat{\text{S.d.}}$	7.03	8.04	7.31	7.70	7.50
			$\widehat{\text{RMSE}}$	9.23	8.05	8.24	7.70	7.50
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-5.98	-0.20	-3.78	0.15	0.17
			$\widehat{\text{S.d.}}$	6.75	7.68	7.00	7.39	7.19
			$\widehat{\text{RMSE}}$	9.01	7.68	7.96	7.39	7.20
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.96	0.12	-3.58	0.44	0.65
			$\widehat{\text{S.d.}}$	53.53	61.44	55.70	59.95	57.28
			$\widehat{\text{RMSE}}$	53.86	61.44	55.81	59.95	57.28
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-6.47	-0.29	-4.04	0.14	0.07
			$\widehat{\text{S.d.}}$	5.59	6.48	5.84	6.28	6.00
			$\widehat{\text{RMSE}}$	8.55	6.49	7.11	6.28	6.00
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-6.54	-0.21	-4.06	0.19	0.15
			$\widehat{\text{S.d.}}$	5.45	6.30	5.70	6.09	5.85
			$\widehat{\text{RMSE}}$	8.51	6.31	7.00	6.09	5.85
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-7.01	0.35	-4.17	0.50	0.69
			$\widehat{\text{S.d.}}$	45.47	53.63	47.89	52.42	49.24
			$\widehat{\text{RMSE}}$	46.01	53.63	48.07	52.42	49.24
	(c)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-7.37	-0.06	-4.37	0.33	0.25
			$\widehat{\text{S.d.}}$	5.21	6.32	5.56	6.07	5.70
			$\widehat{\text{RMSE}}$	9.03	6.32	7.07	6.08	5.71
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-7.70	-0.03	-4.50	0.36	0.28
			$\widehat{\text{S.d.}}$	5.39	6.54	5.75	6.35	5.92
			$\widehat{\text{RMSE}}$	9.40	6.54	7.30	6.36	5.93
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-9.88	0.17	-5.33	0.59	0.48
			$\widehat{\text{S.d.}}$	46.54	58.08	50.38	56.83	51.81
			$\widehat{\text{RMSE}}$	47.58	58.08	50.66	56.83	51.81
II	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.91	0.61	-3.39	0.92	0.79
			$\widehat{\text{S.d.}}$	5.98	6.98	6.25	6.73	6.43
			$\widehat{\text{RMSE}}$	8.41	7.00	7.11	6.79	6.47
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-5.96	0.78	-3.33	1.11	0.91
			$\widehat{\text{S.d.}}$	5.87	6.93	6.18	6.68	6.32

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\text{RMSE}}$	8.36	6.97	7.02	6.77	6.39
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-6.30	1.98	-2.94	2.37	1.75
			$\widehat{\text{S.d.}}$	48.76	58.21	51.55	57.12	53.01
			$\widehat{\text{RMSE}}$	49.16	58.24	51.63	57.17	53.04
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-11.47	-5.94	-9.32	-5.43	-5.39
			$\widehat{\text{S.d.}}$	5.23	6.05	5.45	5.82	5.60
			$\widehat{\text{RMSE}}$	12.61	8.48	10.79	7.96	7.77
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-12.27	-6.69	-10.07	-6.15	-6.12
			$\widehat{\text{S.d.}}$	5.04	5.85	5.29	5.64	5.40
			$\widehat{\text{RMSE}}$	13.26	8.88	11.37	8.34	8.16
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-17.55	-11.68	-15.06	-10.96	-10.99
			$\widehat{\text{S.d.}}$	41.50	48.42	43.49	47.47	44.79
			$\widehat{\text{RMSE}}$	45.05	49.81	46.02	48.72	46.11
III	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-11.28	-12.68	-10.51	-7.41	-5.95
			$\widehat{\text{S.d.}}$	5.47	5.97	5.67	5.89	5.88
			$\widehat{\text{RMSE}}$	12.54	14.02	11.95	9.46	8.36
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-11.77	-13.18	-11.01	-8.01	-6.45
			$\widehat{\text{S.d.}}$	5.48	5.95	5.67	5.91	5.90
			$\widehat{\text{RMSE}}$	12.98	14.46	12.38	9.96	8.74
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.00	-16.49	-14.31	-12.04	-9.81
			$\widehat{\text{S.d.}}$	45.96	49.87	47.45	49.58	48.88
			$\widehat{\text{RMSE}}$	48.35	52.52	49.55	51.02	49.85
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-17.90	-19.20	-17.27	-14.21	-13.02
			$\widehat{\text{S.d.}}$	4.60	5.04	4.76	4.98	4.92
			$\widehat{\text{RMSE}}$	18.48	19.85	17.91	15.06	13.92
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-19.18	-20.48	-18.58	-15.64	-14.38
			$\widehat{\text{S.d.}}$	4.45	4.87	4.60	4.80	4.77
			$\widehat{\text{RMSE}}$	19.69	21.05	19.14	16.36	15.15
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-27.70	-29.05	-27.30	-25.16	-23.43
			$\widehat{\text{S.d.}}$	37.04	40.14	38.15	40.47	39.27
			$\widehat{\text{RMSE}}$	46.25	49.55	46.91	47.65	45.73

Table B3. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of large stands (10% divided plots). Here, $\lambda_2 = 1.15\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.15	0.06	-1.32	0.20	0.20
			$\widehat{\mathrm{S.d.}}$	7.07	7.45	7.17	7.34	7.24
			$\widehat{\mathrm{RMSE}}$	7.39	7.45	7.29	7.35	7.24
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-2.22	0.03	-1.38	0.16	0.15
			$\widehat{\mathrm{S.d.}}$	6.79	7.17	6.88	7.07	6.96
			$\widehat{\mathrm{RMSE}}$	7.15	7.17	7.01	7.07	6.96
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.71	-0.19	-1.77	-0.15	-0.15
			$\widehat{\mathrm{S.d.}}$	54.09	57.48	54.96	56.86	55.54
			$\widehat{\mathrm{RMSE}}$	54.15	57.48	54.99	56.86	55.53
	(b)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.40	0.01	-1.46	0.18	0.16
			$\widehat{\mathrm{S.d.}}$	5.77	6.11	5.85	6.02	5.92
			$\widehat{\mathrm{RMSE}}$	6.24	6.11	6.03	6.02	5.92
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-2.39	0.07	-1.43	0.25	0.23
			$\widehat{\mathrm{S.d.}}$	5.63	5.99	5.74	5.90	5.79
			$\widehat{\mathrm{RMSE}}$	6.12	5.99	5.91	5.91	5.79
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.35	0.41	-1.24	0.73	0.70
			$\widehat{\mathrm{S.d.}}$	46.94	50.04	47.93	49.64	48.41
			$\widehat{\mathrm{RMSE}}$	46.99	50.04	47.94	49.65	48.41
	(c)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.81	0.13	-1.61	0.27	0.24
			$\widehat{\mathrm{S.d.}}$	5.52	5.94	5.65	5.86	5.72
			$\widehat{\mathrm{RMSE}}$	6.19	5.94	5.88	5.87	5.72
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-2.80	0.33	-1.52	0.44	0.41
			$\widehat{\mathrm{S.d.}}$	5.65	6.09	5.78	6.02	5.87
			$\widehat{\mathrm{RMSE}}$	6.31	6.10	5.98	6.04	5.88
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-2.76	1.68	-0.86	1.57	1.61
			$\widehat{\mathrm{S.d.}}$	50.02	54.50	51.37	54.07	52.22
			$\widehat{\mathrm{RMSE}}$	50.09	54.52	51.37	54.09	52.24
II	(a)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-1.97	0.56	-1.02	0.69	0.64
			$\widehat{\mathrm{S.d.}}$	6.13	6.50	6.23	6.43	6.30
			$\widehat{\mathrm{RMSE}}$	6.44	6.52	6.31	6.46	6.33
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-1.92	0.71	-0.91	0.86	0.77
			$\widehat{\mathrm{S.d.}}$	6.01	6.41	6.11	6.31	6.19

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\mathrm{RMSE}}$	6.31	6.45	6.18	6.36	6.23
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-1.53	1.69	-0.18	2.00	1.68
			$\widehat{\mathrm{S.d.}}$	50.53	54.23	51.55	53.81	52.23
			$\widehat{\mathrm{RMSE}}$	50.55	54.25	51.55	53.84	52.25
	(b)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-8.03	-5.89	-7.21	-5.66	-5.67
			$\widehat{\mathrm{S.d.}}$	5.32	5.61	5.40	5.54	5.46
			$\widehat{\mathrm{RMSE}}$	9.63	8.13	9.01	7.93	7.87
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-8.84	-6.69	-8.01	-6.46	-6.45
			$\widehat{\mathrm{S.d.}}$	5.11	5.40	5.18	5.32	5.24
			$\widehat{\mathrm{RMSE}}$	10.21	8.60	9.54	8.37	8.32
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-14.26	-12.00	-13.30	-11.79	-11.70
			$\widehat{\mathrm{S.d.}}$	42.51	45.05	43.18	44.74	43.76
			$\widehat{\mathrm{RMSE}}$	44.83	46.62	45.18	46.27	45.30
III	(a)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-5.74	-7.24	-5.71	-4.39	-3.82
			$\widehat{\mathrm{S.d.}}$	5.82	5.97	5.88	5.95	5.97
			$\widehat{\mathrm{RMSE}}$	8.18	9.38	8.20	7.39	7.09
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-5.94	-7.41	-5.91	-4.66	-4.04
			$\widehat{\mathrm{S.d.}}$	5.78	5.89	5.82	5.91	5.93
			$\widehat{\mathrm{RMSE}}$	8.29	9.47	8.30	7.53	7.18
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-7.29	-8.60	-7.29	-6.50	-5.54
			$\widehat{\mathrm{S.d.}}$	48.41	49.43	48.79	49.49	49.35
			$\widehat{\mathrm{RMSE}}$	48.95	50.17	49.33	49.91	49.65
	(b)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-12.09	-13.44	-12.06	-10.73	-10.29
			$\widehat{\mathrm{S.d.}}$	4.96	5.10	5.02	5.10	5.08
			$\widehat{\mathrm{RMSE}}$	13.07	14.38	13.06	11.88	11.47
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-13.16	-14.48	-13.14	-11.88	-11.40
			$\widehat{\mathrm{S.d.}}$	4.82	4.92	4.86	4.95	4.94
			$\widehat{\mathrm{RMSE}}$	14.02	15.30	14.01	12.87	12.42
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-20.32	-21.40	-20.34	-19.54	-18.82
			$\widehat{\mathrm{S.d.}}$	39.88	40.78	40.23	41.00	40.65
			$\widehat{\mathrm{RMSE}}$	44.76	46.05	45.08	45.42	44.79

Table B4. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of small stands (50% divided plots). Here, $\lambda_2 = 1.4\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-12.70	-0.60	-7.91	0.13	0.10
			$\widehat{\text{S.d.}}$	6.77	9.19	7.41	8.34	7.78
			$\widehat{\text{RMSE}}$	14.39	9.21	10.84	8.34	7.78
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-13.04	-0.65	-8.09	0.17	0.08
			$\widehat{\text{S.d.}}$	5.99	8.24	6.62	7.45	6.90
			$\widehat{\text{RMSE}}$	14.35	8.27	10.45	7.45	6.90
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.88	-0.76	-8.53	0.26	0.01
			$\widehat{\text{S.d.}}$	21.54	29.90	23.83	27.70	24.99
			$\widehat{\text{RMSE}}$	25.62	29.91	25.31	27.70	24.99
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.44	-0.55	-8.27	0.27	0.15
			$\widehat{\text{S.d.}}$	5.41	7.61	5.98	6.83	6.29
			$\widehat{\text{RMSE}}$	14.49	7.63	10.20	6.83	6.30
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-14.02	-0.43	-8.44	0.44	0.26
			$\widehat{\text{S.d.}}$	5.00	7.13	5.61	6.48	5.88
			$\widehat{\text{RMSE}}$	14.89	7.14	10.13	6.50	5.89
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.47	-0.12	-8.87	0.84	0.55
			$\widehat{\text{S.d.}}$	18.32	26.69	20.66	24.55	21.80
			$\widehat{\text{RMSE}}$	23.98	26.69	22.48	24.57	21.81
	(c)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.17	-0.58	-9.04	0.38	0.15
			$\widehat{\text{S.d.}}$	4.87	7.24	5.55	6.62	5.84
			$\widehat{\text{RMSE}}$	15.94	7.27	10.61	6.63	5.84
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-16.41	-0.01	-9.40	0.86	0.50
			$\widehat{\text{S.d.}}$	5.04	8.20	5.92	7.44	6.25
			$\widehat{\text{RMSE}}$	17.17	8.20	11.11	7.49	6.27
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-19.51	1.42	-10.30	2.05	1.39
			$\widehat{\text{S.d.}}$	18.69	31.10	22.44	28.61	23.57
			$\widehat{\text{RMSE}}$	27.01	31.13	24.69	28.68	23.61
II	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-13.04	0.21	-7.73	1.16	0.77
			$\widehat{\text{S.d.}}$	5.76	8.14	6.42	7.41	6.75
			$\widehat{\text{RMSE}}$	14.25	8.14	10.05	7.50	6.79
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-13.64	0.66	-7.84	1.44	0.95
			$\widehat{\text{S.d.}}$	5.38	8.03	6.12	7.27	6.40

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\mathrm{RMSE}}$	14.66	8.06	9.95	7.41	6.47
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-15.14	1.79	-8.12	2.16	1.41
			$\widehat{\mathrm{S.d.}}$	19.62	29.62	22.45	27.35	23.56
			$\widehat{\mathrm{RMSE}}$	24.78	29.67	23.87	27.43	23.60
	(b)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-17.77	-6.47	-13.16	-5.22	-5.09
			$\widehat{\mathrm{S.d.}}$	5.12	7.08	5.68	6.41	5.95
			$\widehat{\mathrm{RMSE}}$	18.49	9.59	14.33	8.27	7.83
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-19.98	-8.62	-15.26	-7.23	-7.09
			$\widehat{\mathrm{S.d.}}$	4.52	6.45	5.05	5.86	5.30
			$\widehat{\mathrm{RMSE}}$	20.49	10.77	16.08	9.30	8.86
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-25.51	-13.99	-20.52	-12.24	-12.10
			$\widehat{\mathrm{S.d.}}$	16.59	23.58	18.51	22.04	19.58
			$\widehat{\mathrm{RMSE}}$	30.43	27.41	27.63	25.21	23.02
III	(a)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-16.03	-10.20	-11.88	-4.71	-2.50
			$\widehat{\mathrm{S.d.}}$	5.28	7.64	5.92	8.10	6.33
			$\widehat{\mathrm{RMSE}}$	16.88	12.75	13.27	9.37	6.80
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-16.81	-8.37	-11.84	-2.28	-2.35
			$\widehat{\mathrm{S.d.}}$	6.22	22.77	11.12	24.69	9.01
			$\widehat{\mathrm{RMSE}}$	17.92	24.26	16.24	24.80	9.32
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-18.76	-3.77	-11.74	3.80	-1.99
			$\widehat{\mathrm{S.d.}}$	22.91	79.72	39.52	86.02	32.46
			$\widehat{\mathrm{RMSE}}$	29.61	79.80	41.22	86.10	32.52
	(b)	$\hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-23.41	-19.07	-20.18	-13.78	-11.67
			$\widehat{\mathrm{S.d.}}$	4.25	5.70	4.69	5.31	4.99
			$\widehat{\mathrm{RMSE}}$	23.79	19.90	20.71	14.77	12.69
		$\hat{\lambda}_2$	$\widehat{\mathrm{Bias}}$	-26.69	-22.65	-23.51	-17.42	-15.00
			$\widehat{\mathrm{S.d.}}$	3.99	5.47	4.47	5.04	4.77
			$\widehat{\mathrm{RMSE}}$	26.99	23.30	23.93	18.14	15.74
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\mathrm{Bias}}$	-34.89	-31.61	-31.83	-26.54	-23.32
			$\widehat{\mathrm{S.d.}}$	14.89	19.91	16.58	19.14	17.64
			$\widehat{\mathrm{RMSE}}$	37.94	37.35	35.89	32.72	29.24

Table B5. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of intermediate stands (25% divided plots). Here, $\lambda_2 = 1.4\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.94	-0.24	-3.78	0.17	0.14
			$\widehat{\text{S.d.}}$	6.95	7.94	7.20	7.65	7.41
			$\widehat{\text{RMSE}}$	9.15	7.94	8.13	7.65	7.41
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-6.18	-0.28	-3.91	0.13	0.08
			$\widehat{\text{S.d.}}$	6.20	7.10	6.44	6.85	6.61
			$\widehat{\text{RMSE}}$	8.75	7.10	7.53	6.85	6.61
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-6.78	-0.37	-4.26	0.02	-0.08
			$\widehat{\text{S.d.}}$	22.39	25.82	23.29	25.16	24.00
			$\widehat{\text{RMSE}}$	23.40	25.82	23.67	25.15	23.99
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-6.41	-0.20	-3.95	0.19	0.14
			$\widehat{\text{S.d.}}$	5.60	6.49	5.86	6.25	6.01
			$\widehat{\text{RMSE}}$	8.51	6.50	7.07	6.25	6.01
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-6.87	-0.29	-4.23	0.08	0.07
			$\widehat{\text{S.d.}}$	5.32	6.23	5.59	6.01	5.74
			$\widehat{\text{RMSE}}$	8.69	6.24	7.01	6.01	5.74
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-8.04	-0.51	-4.93	-0.17	-0.12
			$\widehat{\text{S.d.}}$	19.67	23.23	20.78	22.65	21.36
			$\widehat{\text{RMSE}}$	21.25	23.23	21.36	22.65	21.36
	(c)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-7.37	-0.06	-4.36	0.33	0.25
			$\widehat{\text{S.d.}}$	5.22	6.31	5.57	6.06	5.70
			$\widehat{\text{RMSE}}$	9.03	6.31	7.08	6.07	5.71
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-8.13	0.31	-4.58	0.69	0.52
			$\widehat{\text{S.d.}}$	5.61	7.09	6.06	6.81	6.25
			$\widehat{\text{RMSE}}$	9.88	7.10	7.59	6.84	6.27
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-10.06	1.22	-5.12	1.60	1.18
			$\widehat{\text{S.d.}}$	21.19	27.19	23.12	26.19	23.86
			$\widehat{\text{RMSE}}$	23.46	27.21	23.68	26.23	23.89
II	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.99	0.49	-3.48	0.82	0.67
			$\widehat{\text{S.d.}}$	5.99	7.00	6.27	6.75	6.44
			$\widehat{\text{RMSE}}$	8.47	7.02	7.17	6.80	6.48
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-6.37	0.64	-3.61	0.97	0.75
			$\widehat{\text{S.d.}}$	5.79	6.93	6.12	6.67	6.28

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\text{RMSE}}$	8.61	6.96	7.10	6.74	6.33
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-7.32	1.02	-3.94	1.35	0.94
			$\widehat{\text{S.d.}}$	21.50	25.96	22.83	25.22	23.48
			$\widehat{\text{RMSE}}$	22.72	25.98	23.17	25.25	23.50
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-11.53	-6.02	-9.38	-5.50	-5.47
			$\widehat{\text{S.d.}}$	5.26	6.11	5.49	5.85	5.64
			$\widehat{\text{RMSE}}$	12.67	8.58	10.87	8.03	7.86
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-13.86	-8.32	-11.66	-7.72	-7.67
			$\widehat{\text{S.d.}}$	4.80	5.62	5.04	5.40	5.18
			$\widehat{\text{RMSE}}$	14.67	10.04	12.70	9.42	9.25
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-19.68	-14.05	-17.35	-13.25	-13.15
			$\widehat{\text{S.d.}}$	17.86	20.89	18.78	20.44	19.33
			$\widehat{\text{RMSE}}$	26.58	25.18	25.56	24.36	23.37
III	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-11.17	-12.62	-10.42	-7.28	-5.81
			$\widehat{\text{S.d.}}$	5.44	5.93	5.62	5.88	5.86
			$\widehat{\text{RMSE}}$	12.43	13.94	11.84	9.36	8.25
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-12.30	-13.76	-11.59	-8.78	-6.96
			$\widehat{\text{S.d.}}$	5.53	6.09	5.75	6.02	6.02
			$\widehat{\text{RMSE}}$	13.48	15.04	12.94	10.64	9.20
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.11	-16.60	-14.52	-12.53	-9.83
			$\widehat{\text{S.d.}}$	20.69	22.69	21.47	22.56	22.20
			$\widehat{\text{RMSE}}$	25.62	28.12	25.92	25.80	24.28
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-17.82	-19.15	-17.20	-14.14	-12.94
			$\widehat{\text{S.d.}}$	4.54	4.99	4.68	4.89	4.86
			$\widehat{\text{RMSE}}$	18.39	19.79	17.83	14.97	13.82
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-21.13	-22.44	-20.59	-17.84	-16.46
			$\widehat{\text{S.d.}}$	4.19	4.58	4.32	4.51	4.49
			$\widehat{\text{RMSE}}$	21.55	22.90	21.04	18.40	17.06
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-29.43	-30.66	-29.07	-27.09	-25.25
			$\widehat{\text{S.d.}}$	15.75	17.13	16.24	17.00	16.73
			$\widehat{\text{RMSE}}$	33.38	35.12	33.30	31.99	30.29

Table B6. Bias (%), standard deviation (S.d. %), and RMSE (%) of the estimators in the case of large stands (10% divided plots). Here, $\lambda_2 = 1.4\lambda_1$. In Case I the plant populations follow a homogeneous Poisson process across the entire landscape, and in Case II and Case III the densities vary between different strata (in subcase a stratum identifiers were known and could be utilized in estimators, whereas identifiers were not available in subcase b). In Case II the densities were the same in all parts of a stratum whereas in Case III the densities were doubled in a 10 m wide zone along all stand boundaries.

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
I	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-2.28	-0.09	-1.47	0.07	0.07
			$\widehat{\text{S.d.}}$	7.17	7.53	7.26	7.43	7.34
			$\widehat{\text{RMSE}}$	7.52	7.53	7.41	7.43	7.34
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-2.30	-0.04	-1.44	0.12	0.13
			$\widehat{\text{S.d.}}$	6.34	6.66	6.43	6.58	6.49
			$\widehat{\text{RMSE}}$	6.74	6.66	6.59	6.58	6.49
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-2.34	0.09	-1.39	0.23	0.28
			$\widehat{\text{S.d.}}$	23.01	24.40	23.39	24.15	23.63
			$\widehat{\text{RMSE}}$	23.13	24.40	23.43	24.15	23.63
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-2.41	0.01	-1.48	0.12	0.14
			$\widehat{\text{S.d.}}$	5.73	6.05	5.82	6.00	5.88
			$\widehat{\text{RMSE}}$	6.22	6.05	6.00	6.00	5.88
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-2.58	0.04	-1.57	0.14	0.14
			$\widehat{\text{S.d.}}$	5.48	5.81	5.57	5.76	5.64
			$\widehat{\text{RMSE}}$	6.06	5.81	5.79	5.76	5.64
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-3.01	0.12	-1.77	0.20	0.16
			$\widehat{\text{S.d.}}$	20.21	21.52	20.60	21.41	20.86
			$\widehat{\text{RMSE}}$	20.43	21.52	20.68	21.41	20.86
	(c)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-2.83	0.09	-1.65	0.22	0.21
			$\widehat{\text{S.d.}}$	5.51	5.92	5.63	5.83	5.70
			$\widehat{\text{RMSE}}$	6.19	5.92	5.86	5.83	5.70
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-2.98	0.46	-1.54	0.61	0.54
			$\widehat{\text{S.d.}}$	6.06	6.67	6.28	6.58	6.35
			$\widehat{\text{RMSE}}$	6.75	6.68	6.46	6.61	6.37
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-3.37	1.40	-1.28	1.59	1.37
			$\widehat{\text{S.d.}}$	22.93	25.16	23.77	24.93	24.09
			$\widehat{\text{RMSE}}$	23.18	25.20	23.81	24.98	24.12
II	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-1.94	0.64	-0.98	0.76	0.68
			$\widehat{\text{S.d.}}$	6.17	6.57	6.27	6.46	6.35
			$\widehat{\text{RMSE}}$	6.47	6.60	6.35	6.51	6.38
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-1.85	0.98	-0.75	1.09	0.99
			$\widehat{\text{S.d.}}$	5.94	6.36	6.07	6.30	6.14

Case	Subcase	Estimator		Method				
				BASELINE	*THRESHOLD90*	*THRESHOLD60*	*RECALCULATION*	*REGRESSION*
			$\widehat{\text{RMSE}}$	6.22	6.44	6.12	6.39	6.21
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-1.62	1.83	-0.16	1.90	1.76
			$\widehat{\text{S.d.}}$	22.24	23.95	22.75	23.72	23.04
			$\widehat{\text{RMSE}}$	22.30	24.01	22.75	23.79	23.10
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-8.04	-5.86	-7.24	-5.68	-5.68
			$\widehat{\text{S.d.}}$	5.36	5.68	5.45	5.59	5.50
			$\widehat{\text{RMSE}}$	9.67	8.16	9.06	7.97	7.91
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-10.20	-7.98	-9.34	-7.78	-7.77
			$\widehat{\text{S.d.}}$	4.88	5.17	4.96	5.10	5.02
			$\widehat{\text{RMSE}}$	11.31	9.51	10.57	9.30	9.25
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-15.59	-13.28	-14.60	-13.03	-12.98
			$\widehat{\text{S.d.}}$	18.19	19.31	18.48	19.23	18.75
			$\widehat{\text{RMSE}}$	23.96	23.43	23.55	23.23	22.80
III	(a)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-5.68	-7.19	-5.65	-4.32	-3.75
			$\widehat{\text{S.d.}}$	5.76	5.89	5.80	5.89	5.90
			$\widehat{\text{RMSE}}$	8.09	9.29	8.10	7.30	6.99
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-6.18	-7.57	-6.14	-5.01	-4.29
			$\widehat{\text{S.d.}}$	5.86	5.98	5.91	6.00	6.02
			$\widehat{\text{RMSE}}$	8.52	9.65	8.53	7.82	7.40
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-7.42	-8.54	-7.36	-6.73	-5.63
			$\widehat{\text{S.d.}}$	21.70	22.15	21.91	22.21	22.17
			$\widehat{\text{RMSE}}$	22.93	23.74	23.11	23.21	22.87
	(b)	$\hat{\lambda}_1$	$\widehat{\text{Bias}}$	-12.06	-13.42	-12.04	-10.72	-10.26
			$\widehat{\text{S.d.}}$	4.93	5.06	4.97	5.06	5.05
			$\widehat{\text{RMSE}}$	13.03	14.35	13.02	11.86	11.44
		$\hat{\lambda}_2$	$\widehat{\text{Bias}}$	-14.85	-16.09	-14.83	-13.68	-13.15
			$\widehat{\text{S.d.}}$	4.60	4.70	4.64	4.71	4.71
			$\widehat{\text{RMSE}}$	15.55	16.76	15.53	14.47	13.97
		$\hat{\lambda}_2 - \hat{\lambda}_1$	$\widehat{\text{Bias}}$	-21.85	-22.74	-21.80	-21.09	-20.37
			$\widehat{\text{S.d.}}$	17.03	17.38	17.17	17.46	17.36
			$\widehat{\text{RMSE}}$	27.70	28.62	27.75	27.38	26.77