Uncertainty of Large-Area Estimates of Indicators of Forest Structural Gamma Diversity: A Study Based on National Forest Inventory Data

Susanne Winter, Andreas Böck, and Ronald E. McRoberts

Abstract: Tree diameter and height are commonly measured forest structural variables, and indicators based on them are candidates for assessing forest diversity. We conducted our study on the uncertainty of estimates for mostly large geographic scales for four indicators of forest structural gamma diversity: mean tree diameter, mean tree height, and standard deviations of tree diameter and tree height. We had three objectives: to estimate the number of national forest inventory (NFI) plots whose data must be aggregated to obtain precise estimates of the indicators of gamma forest structural diversity; to assess differences in structural associations with respect to different forest categories; and to assess the effects of geographic distance on estimates of indicators of forest structural diversity. Uncertainty assessments were conducted using a bootstrap resampling approach and a geospatial approach to assess the effects of geographic distances. Our study relied on a database populated with NFI plot data (12,536 plots and 256,513 trees) from 13 European countries and three ecoprovinces of the United States. The results were threefold. First, data from approximately 150 NFI plots randomly selected from a large database are generally sufficient to estimate standard deviations (SDs) of diameter and height as indicators of structural forest diversity at large scales with acceptable precision. Second, the uncertainties of the estimates were generally greater for forest categories in Europe than in the United States with the exception of Douglas fir forests in the Pacific Northwest of the United States. Third, diameter and height gamma diversities expressed by the means and SDs of distributions of tree diameter and tree height were more similar for geographic areas separated by smaller distances. FOR. SCI. 58(3):284–293.

Keywords: national forest inventory, international reporting on biodiversity, tree diameter and height, spatial autocorrelation

FOREST STRUCTURE, DEFINED AS THE PHYSICAL ORGANIZATION of forest elements with respect to composition and complexity, is an important feature of forest diversity (Chirici et al. 2012), and greater forest structural heterogeneity is understood to be a prerequisite for greater biodiversity of forest plants and animals (Paillet et al. 2010). Old-growth forests exhibit large structural heterogeneity (e.g., small gaps, different tree dimensions and densities, mortality processes, distribution of deadwood, and natural regeneration) resulting from structural differentiations within natural life cycles caused by phenomena such as natural disturbances and tree competition. Large structural heterogeneity in managed forests produces high rankings of naturalness (Bartha 2004, Winter et al. 2010), is positively correlated with the diversity of forest flora and fauna, and has a large positive impact on numbers of lichens, bryophytes, and bird and coleopteran species and their population sizes (De Graaf et al. 1998, Schumacher 2006, Müller et al. 2007, Winter and Möller 2008, Müller and Brandl 2009). The intensity of animal and plant species uses of trees for purposes such as breeding, foraging, and habitat increases with greater tree diameter and height and is well documented for boreal forests by Liira and Kohv (2010), for oaks by Wolf et al. (2009), for Douglas-fir (*Pseudotsuga menziesii* var. *Menziesii*) forests in the western United States by Michel et al. (2011), for beech forests (*Fagus sylvatica* L.) by Winter and Möller (2008), and for alpine spruce forests by Nascimbene et al. (2009). In addition, injured, hollow, and dying trees of large dimensions support saproxylic beetle assemblages and red-listed lichens (Okland et al. 1996, Ranius et al. 2007, Moning et al. 2009), although small trees still provide habitats but to a lesser extent than do large trees (Nascimbene et al. 2009). The insight of the positive correlation between large trees and greater overall forest biodiversity was gained from programs whose aims included ensuring large tree continuity and structural heterogeneity as seen in managed forests in Germany (Jedicke 1977, Zabel 2006) and maintaining old-growth forest as seen for Douglas-fir forests in the northwestern United States (Brodie et al. 2007).

National forest inventories (NFI) as conducted in Europe and North America and increasingly in Asia and South

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America are the most comprehensive and extensive sources of data that can be used to assess forest structural diversity. Chirici et al. (2012) demonstrate that NFIs routinely acquire data for multiple variables that might be suitable for assessing and reporting forest diversity. dbh (mostly measured at 1.3-m tree height in Europe and at 1.37-m height in the United States) and height (ht) are the most commonly measured variables assessed by NFIs that can be used to describe forest structure (Winter et al. 2008, Tomppo et al. 2010). However, neither variable is proposed as important for inclusion in biodiversity indicators by investigators such as Larsson et al. (2001). The indicator list for sustainable forest management proposed by the Ministerial Conference on the Protection of Forests in Europe ([MCPFE] 2002) includes Indicator 1.3, "Age structure and/or diameter distribution," but does not specify a precise definition that can be used for applications of the indicator. The review by McElhinny et al. (2005) on forest structural indicators associated with forest diversity reveals that tree dbh and ht data adequately describe the forest structure of individual stands. Acker et al. (1998) and Michel et al. (2011) showed that the presence of large trees and greater structural diversity are associated with larger numbers of habitat niches and species that use the niches. However, these studies do not propose feasible indicators for large-scale biodiversity monitoring.

Indices for describing forest heterogeneity are often based on variables such as tree dbh and ht (Staudhammer and LeMay 2001, Pommerening 2002, Varga et al. 2005, Pretzsch 2009). Numerous studies focus on dbh distributions characterized using Weibull (Bailey and Dell 1973) and other density functions (e.g., Johnson 1949, Fonseca et al. 2009). Fewer studies focus on ht distributions (e.g., Hafley and Schreider 1977, Wand et al. 2008). For biodiversity monitoring and reporting at large regional scales up to the continental level, dhb and ht distribution functions are generally not suitable for analyses because they are too complex and are mostly appropriate only for forest stands or small forested areas (McElhinny et al. 2005) rather than for large scales. Simple indicators for monitoring stand structure dynamics and diversity are required for large-scale biodiversity assessment and reporting. An indicator based on the Shannon index was proposed by Pretzsch (2009, p. 280ff) for comparing forest areas subdivided by dbh or ht classes. The area proportions of the dbh and ht subdivision classes depict the main structural forest composition of smaller regional units such as German provinces or counties in the United States. However, the indicator might not be suitable for very large regional units such as forest categories or continents because summarizing forest structure data by classes might diminish the meaningfulness of the results at large scale. Nevertheless, indicators based on the mean and standard deviation (SD) of tree ht and dbh may augment indicators based on species composition and deadwood for characterizing the heterogeneity of forests at different geographic scales.

The diversity of dbh, quantified as the SD of tree dbh for a sample, increases with the presence of very old and very large trees. The diversity of ht is also expected to increase with the presence of old and large trees.

For large-scale diversity reporting, a large number of forest structure indicators, including the mean and SD of tree dbh and ht, could be suitable for monitoring the essential components of forest biodiversity. NFI records are mostly plot-based and facilitate estimation of the standard deviations of dbh and ht for plots, which could serve as estimators of alpha or small-scale diversity (Whittaker 1972). Such estimates are usually small for homogeneously structured forests, whereas they are typically large for heterogeneously structured, multilayered forests (e.g., Pretzsch 2009, McRoberts et al. 2012). For large-area approaches, the effects of the spatial distribution of structural alpha diversity on structural gamma diversity, total diversity, is generally unknown. Consider two regions, one with many homogeneous forest stands, albeit with different dbh and ht means, and a second region with many heterogeneous forest stands but with similar dbh and ht means. Although mean structural alpha diversities for the two regions would differ considerably, structural gamma diversities for the two regions may be similar.

Under the assumption that similar levels of overall forest diversity (e.g., flora, fauna, lichens, and deadwood) correspond to similar levels of forest structural gamma diversity, regardless of the spatial distribution of alpha diversities, the objectives of our study were threefold: to estimate the number of NFI plots whose data must be aggregated to obtain sufficiently precise estimates of the indicators of gamma forest structural diversity; to assess differences in structural associations with respect to different forest categories; and to assess the effects of geographic distance on estimates of indicators of forest structural diversity.

Data

Our study on the uncertainty of estimates of indicators of large-scale forest structural diversity used a database populated with NFI plot data that was constructed by COST Action E43, "Harmonisation of National Forest Inventories in Europe: Techniques for Common Reporting," conducted under the auspices of the European program, Cooperation in Science and Technology (COST) (COST 2009). The COST Action E43 database (Chirici et al. 2011) included structural data for 256,513 trees from 12,536 NFI forest plots obtained from 14 countries: Austria, Belgium, Czech Republic, Denmark, Finland, Germany, Ireland, Italy, Norway, Portugal, Spain, Sweden, Switzerland, and the United States. Although there may be slight effects due to different sampling protocols, given the large numbers of plots, the relatively large numbers of countries involved, and the range of spatial distances involved, any effects of differences due to sampling protocols were considered negligible. For example, of the 12,536 plots represented in the database, 1,107 (8.8%) include trees with dbh greater than 350 mm. Such trees are of a size that could cause differences in SDs if they are included with one sampling technique but not with another. Three countries (Austria, Germany, and Finland) of the 14 contributing data use relascope sampling. For this method with the traditional basal area factor 2, the maximum distance from plot center to a tallied tree of dbh 350 mm is 17.5 m. This distance is approximately the same as the

17.8-m radius of a circular plot of 1,000 m^2, which is near the center of the range of radii of plots for countries that use fixed area sampling. Therefore, harmonization of relascope and plot data was deemed unnecessary. In addition, the study has been designed to estimate scale effects rather than absolute values of diversity.

The inventory data from the United States were from three ecoprovinces (Bailey 1976): Ecoprovince 212—Lauretian mixed forest province in the northcentral United States around the Great Lakes; Ecoprovince 231—Southern mixed forest province in the southeastern part of United States; and Ecoprovince 242—Pacific lowland mixed forest province in the western United States including parts of Oregon and Washington. For future reference, the 13 European countries and the 3 American ecoprovinces are collectively designated *regional units*.

Tree dbh is a structural variable measured by all NFIs, although its minimum measurement threshold ranges from 0 mm in Denmark to 120 mm in Switzerland (Winter et al. 2008). For harmonization purposes, a reductive bridge (Ståhl et al. 2012) was used whereby all trees with dbh less than 120 mm were excluded from the analyses (Figure 1A). For the entire database, dbh was characterized by a reverse-J distribution, which is typical for forest stands and features multiple young and small trees with only a few old and large trees (Linder et al. 1997, Siipilehto and Siitonen 2004, Westphal et al. 2006). The ht distribution (Figure 1B) follows a curve shape with a left skewness rather than a reverse-J shape because the minimum tree ht was constrained by a dbh threshold.

For some trees (7.3%) represented in the database, mostly of European species, no valid ht measurements were available. However, because the missing ht measurements were primarily for small trees, simply omitting them from the analyses could contribute to inaccurate results. Therefore, a nonparametric regression method (function gam, in R package mgcv) was used to impute values for the missing ht measurements. First, for each forest category, a nonparametric regression model with dbh as a covariate was fit to all pairs having both dbh and ht measurements. Second, the squared residuals were fit using another nonparametric regression model, again using dbh as a covariate, as means of characterizing heterogeneity of variance. Third, for each tree with a missing ht measurement, ht was predicted using the first nonparametric regression model, a residual was randomly drawn from a Gaussian distribution with mean 0 and variance was predicted from the second nonparametric regression model, and the sum of the ht prediction and random residual was imputed to the tree with the missing ht measurement. After the imputations, for each forest category or forest type correlations between ht and dbh for trees without missing measurements were calculated and compared with correlations calculated using all trees, both with measured ht and with imputed ht. The correlations were similar for all forest categories, indicating that the imputed ht values were appropriate approximate substitutes for the missing ht measurements.

We classified the data with respect to both the regional units and European forest categories or American forest types. The European forest categories were based on the descriptions of the European Environment Agency ([EEA] 2006): 1, Boreal; 2, Hemiboreal; 3, Alpine; 5, Mesophytic deciduous; 6, Beech; 7, Mountainous beech, 8, Thermophilous deciduous; 9, Broadleaved, and 10, Mediterranean coniferous forest. The underlying assumption is that the European zonal forest categories represent a broad climatic gradient from the colder and wetter northeast to the warmer and drier southwestern climate zones. In addition, the zonal forest categories represented in the database by at least 100 NFI plots were assumed to be adequately described by those plots. Forest categories 11 (Mire and swamp) and 13 (Non riverine alder) that originate in azonal abiotic habitat conditions and 14 (Plantation) were also considered. Finally, the data from the three American ecoprovinces included

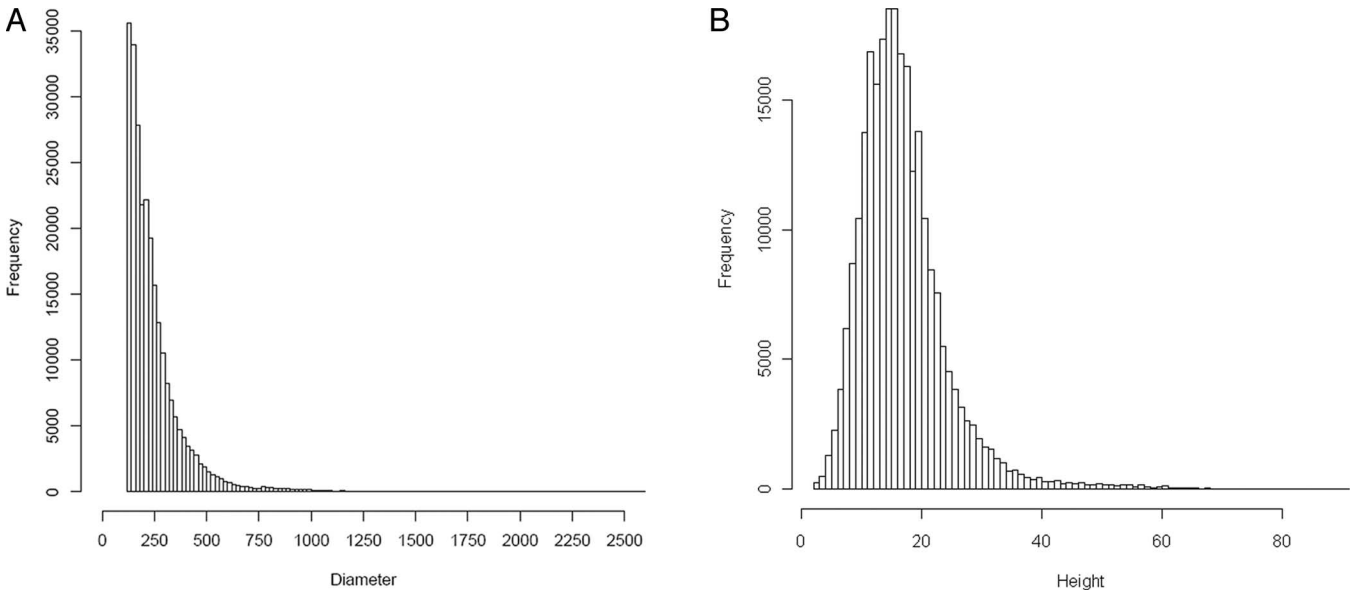

Figure 1. Frequency distribution of tree dbh (mm) (A) and the tree ht (m) (B) for the COST Action E43 test database with 256,213 trees.

five forest types (USDA Forest Service 2011): Loblolly pine (*Pinus taeda*, Forest type 161) from parts of Ecoprovince 231 in the southeastern plantation region, Douglas fir (*Pseudotsuga menziesii*, Forest type 201) from Ecoprovince 242 in the Pacific northwest rainforest region, and aspen (*Populus tremuloides* and *Populus grandidentata*, Forest type 901), paper birch (*Betula papyrifera*, Forest type 902), and balsam poplar (*Populus balsamifera*, Forest type 904) from parts of Ecoprovince 212 in the north central Great Lakes region. For purposes of consistent terminology, the American forest types are henceforth characterized as forest categories.

Methods

Estimates of dbh and ht gamma diversity increase as the number of plots increases (McRoberts et al. 2009), because data for small numbers of randomly selected plots do not adequately represent the range or complexity of entire populations. The explanation is twofold. First, large numbers of small trees are observed on NFI plots because natural forest regeneration is common and is continuously needed to establish future stands. However, the probability of observing large trees on NFI plots is much less than that of observing very small trees. The latter result can be attributed to the effects of competition, natural mortality, and forest management practices that do not place large economic value on the maintenance of large old trees. Thus, very large trees occur mostly in old-growth areas such as forest nature reserves and wilderness areas or as a result of a sustainable forest management that is more ecologically focused. Second, for small homogeneous forest patches, dbh and ht diversities are less than those for larger regions with many different homogeneous forest patches. At large geographic scales, the uncertainty of gamma diversity estimates is large when based on data for only a few plots but is smaller when based on data for many plots. Thus, the first objective of our study was to determine the number of plots needed to obtain estimates of gamma structural diversity with acceptably small uncertainties. Certainly this is one of only a very few assessments of forest structural diversity at such large geographic scales, perhaps because of the lack of appropriate data. As such, we regard it necessary not only to report our results but also to carefully describe our methods. Thus, the underlying aims of the study include demonstration of NFI plot-based approaches for estimating gamma diversity (first objective), for describing general biodiversity differences among forest categories (second objective), and for assessing the effects of geographic distances (third objective).

Our analyses focused on four indicators of forest structural gamma diversity: (1) the mean of the distribution of tree dbh for large areas; (2) the SD of the distribution of tree dbh, denoted s_{dbh}, for large areas; (3) the mean of the distribution of tree ht for large areas; and (4) the SD of the distribution of tree ht, denoted s_{ht}, for large areas. We note here the distinction between estimating large-scale or gamma diversity and small-scale or alpha diversity. By aggregating the data for multiple plots randomly selected from large geographic areas and calculating estimates of indicators without regard to plot affiliation, we are estimating the gamma diversity for the geographic area, whereas if we had estimated the mean of estimates of plot-level indicators, we would have been estimating mean alpha diversity for the area.

The precision of an estimate of an indicator requires knowledge of the SD of the distribution of sample-based estimates of that indicator; in this case, SDs of s_{dbh} and s_{ht}. SDs can be estimated using bootstrap resampling approaches that incorporate Monte Carlo simulation techniques for random resampling from the available data set with replacement after each iteration (Metropolis and Ulam 1949, Hoffman 1998, Efron and Tibshirani 1994). Efron and Tibshirani (1994) recommend at least 200 bootstrap resamples for estimating means but do not address the number of resampling iterations necessary to obtain stable estimates of SDs.

Our analyses took the form of Monte Carlo bootstrap simulations to determine the number of bootstrap resampling iterations and the number of NFI plots necessary to obtain stable estimates of the SDs of large-area distributions of estimates of s_{dbh} and s_{ht}. However, the computational intensity necessary to investigate all possible combinations of number of resampling iterations and number of plots was prohibitive. Preliminary simulations were used to determine just the number of iterations that would be sufficient for SDs of estimates of s_{dbh} and s_{ht} to stabilize, regardless of the number of plots whose data were aggregated. In the main set of simulations we focused on determining the number of plots, given the previously determined number of iterations.

Before implementing the main bootstrap simulations, we subdivided the database into European and American divisions, thereby separating the two main biogeographic regions with their different species populations (Pielou 1972). The numbers of European plots (7,212) and American plots (5,324) were comparable so that comparisons between the two subdivisions were feasible. In addition, the European and American portions of the database were further separately subdivided into forest category classes.

The preliminary simulations were focused on determining the number of bootstrap resampling iterations necessary to obtain stable estimates of the SDs of distributions of estimates of s_{dbh} and s_{ht} for geographic and forest category subdivisions. Stable estimates are necessary to ensure the credibility of results based on the estimates. These simulations took the form of bootstrap resampling iterations and involved repeatedly randomly selecting $m = 5$, 10, 100, and 200 plots from subdivisions, aggregating the data for the m plots without regard to plot affiliation, and calculating estimates of s_{dbh}, and s_{ht}. For each value of m, this bootstrap procedure was repeated for $b = 2, 3, 4, \ldots, 5{,}000$ resampling iterations. After completion of the b iterations for each value of m, the SDs of the estimates of s_{dbh}, and s_{ht} over the b iterations were then calculated. For each value of m, the number of bootstrap iterations necessary for the SDs of the estimates to stabilize was noted. The results indicated that $b = 2500$ resampling iterations were sufficient for the SDs to stabilize, regardless of the number of plots, $m \geq 5$, whose data were aggregated.

The main simulations took the form of bootstrap resampling iterations and involved repeatedly randomly selecting plots, aggregating the data for the selected plots without regard to plot affiliation, and calculating estimates of the four chosen indicators. The number of resampling iterations was fixed at $b = 2500$, the number determined from the first set of simulations to produce stable SDs of the distributions of estimates of s_{dbh} and s_{ht}. The number, m, of plots whose data were aggregated ranged from $m = 5$ to the total number in the database, $m = 7{,}212$ plots for Europe and $m = 5{,}324$ plots for the United States. Third, the analyses included mean dbh and mean ht in addition to s_{dbh} and s_{ht}. Further, because of concern for asymmetry in distributions, we assessed medians rather than means of distributions of the four indicators. Precision was quantified by the range between the 20th and 80th percentiles of the distributions of the estimates of the indicators (Figures 3–5).

We conducted additional geospatial analyses that took into account distances between centroids of the regional units whose NFI plots were represented in the database. The geospatial analyses entailed grouping the regional units with respect to the distances among them. For all European countries and the three American ecoprovinces, the coordinates of their centroids were used to calculate the distances. The distribution of distances among the regional unit centroids indicated that most regional units were within 2,000 km of the other regional units. However, because of the Atlantic Ocean separating Europe and the United States, we had a gap in distances from approximately 3,500 to 6,500 km. The data for the regional units were grouped by five distance intervals with break points of 150, 1,000, 2,000, and 3,000 km. Among European countries, Finland and Portugal have the maximum separation distance of approximately 3,400 km. The maximum distance from Finland to an ecoprovince in the United States is approximately 12,300 km to the western Ecoprovince 242. The distance groups were chosen to represent a gradient from regional to intercontinental scales. In accordance with the general principles of spatial correlation, we hypothesized that dbh and ht diversities for regional units separated by small distances would be more similar and smaller than the diversities for regional units that were separated by greater distances (Tobler 1970). Consequently, we expected that estimates of indicators of dbh and ht diversity would increase when data were grouped for regional units separated by greater distances (Goslee 2006). Data for all plots for each of the four previously described distance groups were aggregated, and the gamma diversity indicators were estimated.

For all analyses we used the R statistical package, version 2.10.1 (R Development Core Team, 2009), with the gplots package for graphing data (Bolker et al. 2009). Although our analyses were conducted using numbers of plots and distances (km), the graphs used to depict our results use a natural logarithmic (ln) transformation to reduce horizontal scales for numbers of plots and distances between the regional units. To facilitate reference to the figures, we report both the numbers of plots and distances and their natural logarithms.

Results

Number of Iterations

The graphs of the estimates of the SDs of s_{dbh} and s_{ht} versus number of plots obtained from the first set of simulations showed that 2,500 Monte Carlo bootstrap resampling iterations were sufficient to obtain stable SDs of distributions of estimates of both s_{dbh} and s_{ht} (Figure 2). For more iterations or for more than $m = 5$ plots per iteration, changes in the SDs of distributions of estimates of s_{dbh} and s_{ht} were negligible. Consequently, we used 2,500 resampling iterations for the second set of simulations.

Uncertainties of Forest Diversity Estimates

For both the American and European subdivisions, 150 plots ($\ln(150) \approx 5$) were necessary for the medians of the distributions of s_{dbh} estimates to stabilize (Figure 3A). Similarly, medians of the distributions of estimates of s_{ht} and mean ht also stabilized for 150 plots and 55 plots, respectively (Figure 3B and D).

Although the median of the distribution of estimates of mean dbh was larger for the European subdivision than for the American subdivision of the data set (Figure 3C), median dbh stabilized for more than 55 plots ($\ln(55) \approx 4$) for both subdivisions. For the 55-plot minimum, the greater symmetry and generally similar shapes of distributions of estimates of mean dbh led to more precise estimates of the indicator. For 55 plots, the range between the 20th and 80th percentiles of the distribution of estimates of mean dbh for the European data was slightly smaller (28.0 mm) than for the American data (31.8 mm, Figure 3C). Both the median of the distribution of s_{dbh} estimates and the range between the 20th and 80th percentiles of the distribution were clearly larger for the American data.

The median of the distribution of estimates of mean ht was generally greater for the American data (Figure 3C) than for the European data, most likely as a result of the tall trees in the Douglas fir forest community (Figures 4B

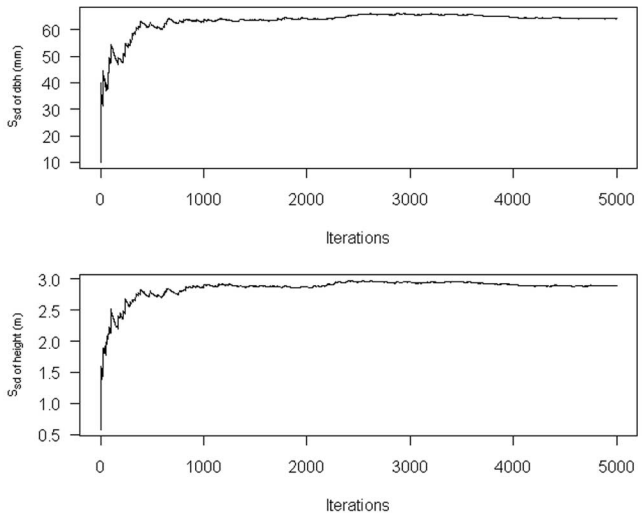

Figure 2. SDs of the SD of dbh (s_{dbh}) (top) and the SD of height (s_{ht}) (bottom) from 2 to 5,000 iterations, where each iteration represents random selection of $m = 5$ plots.

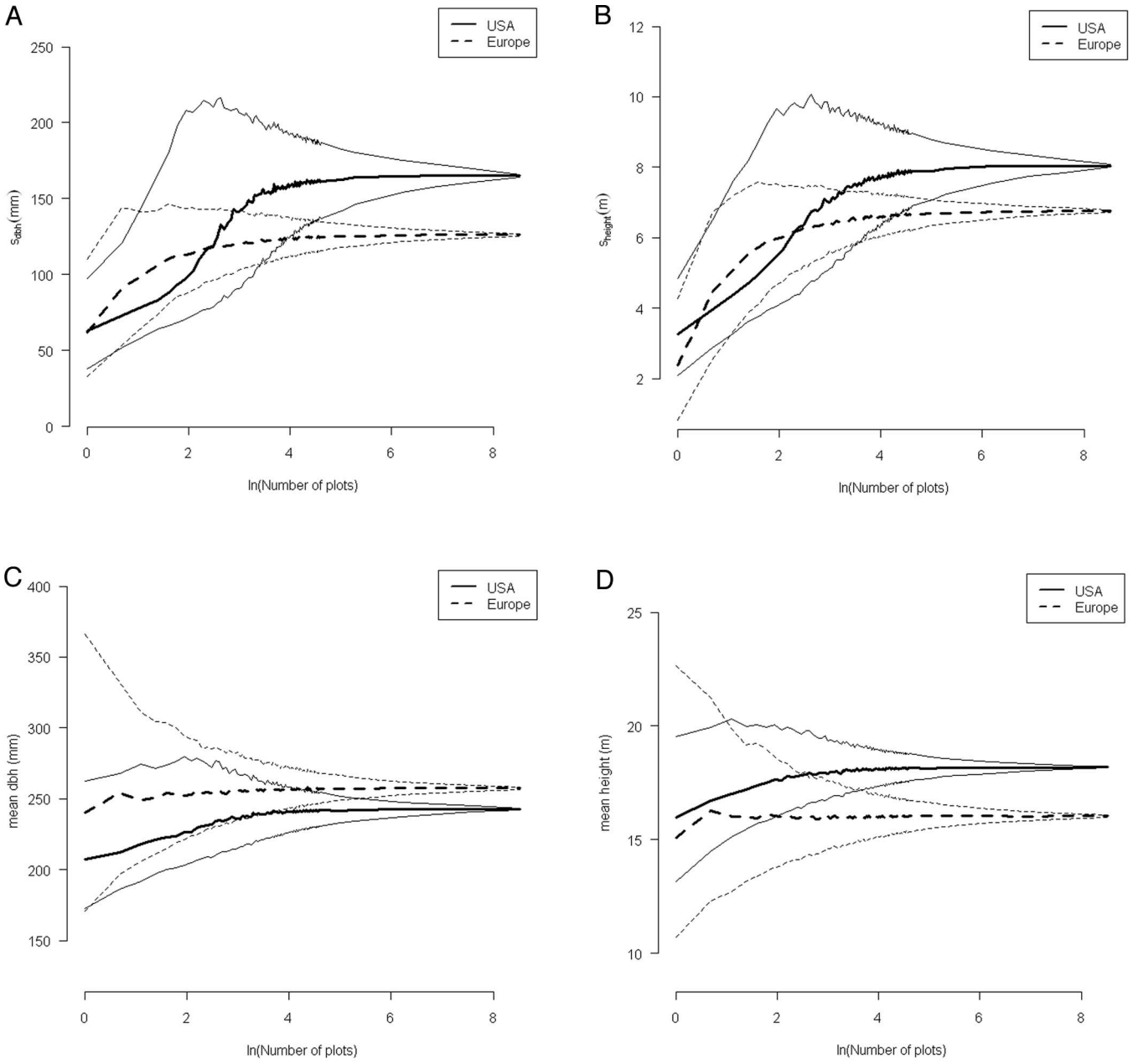

Figure 3. Distributions of means and SDs of indicators estimated using 2,500 bootstrap resampling iterations. Thick lines denote the medians (50th percentile), and thin lines denote the 20th and 80th percentiles: ln(2) ≈ 8; ln(4) ≈ 55; ln(6) ≈ 400; and ln(3,000) ≈ 8. A. s_{dbh}. B. s_{ht}. C. Mean dbh. D. Mean height.

and 5B). The uncertainty of s_{ht} as reflected in the range between the 20th and 80th percentiles of the distribution of its estimates was also mostly greater for the United States (Figure 3D). Tree dbh and ht were correlated but more weakly for the European subdivision of the data set ($r = 0.675$) than for the American subdivision ($r = 0.825$).

Graphs of the medians of s_{dbh} versus number of plots for the European forest categories exhibited almost the same curve shape for each forest category (Figure 4A) with the exception of the azonal Mire and swamp forests (Forest category 11) and the Non riverine alder forests (Forest category 13). Both these azonal forest categories include multiple forest communities with distinctively different growth characteristics, which result in different curve shapes compared with the zonal forest categories. The distinctiveness of the medians for the zonal forest categories confirms the usefulness of the categories as separate classes for reporting purposes. For European forest categories, the median of the distribution of estimates of s_{dbh} can be precisely estimated using a minimum of 7–20 plots (ln(7) ≈ 2, ln(20) ≈ 3) with fewer plots producing underestimates (Figure 4A). Beech forest (Forest category 6) and Mountainous beech forest (forest category 7) are considerably more diverse with respect to dbh than all the other forest categories. For the American forest categories (Figure 4B), the median of s_{dbh} could be precisely estimated using only 5–7 plots (ln(5) ≈ 1.6, ln(7) ≈ 2). However, the

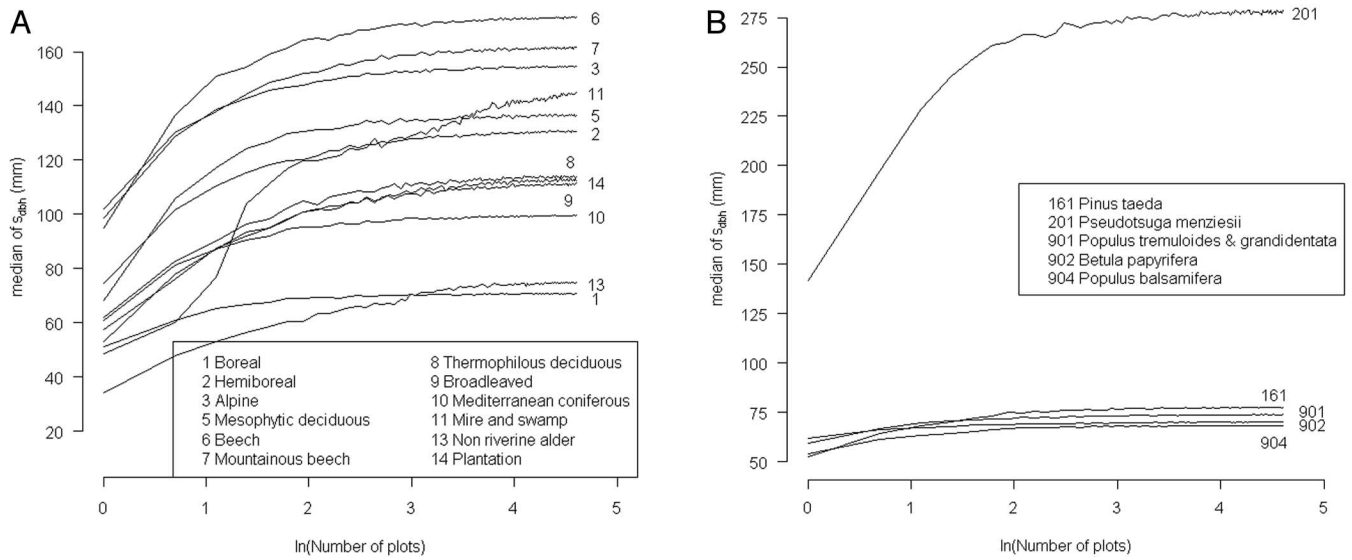

Figure 4. Medians of s_{dbh} for European (A) and American (B) forest categories: ln(2) ≈ 8; ln(4) ≈ 55; ln(6) ≈ 400; and ln(3,000) ≈ 8.

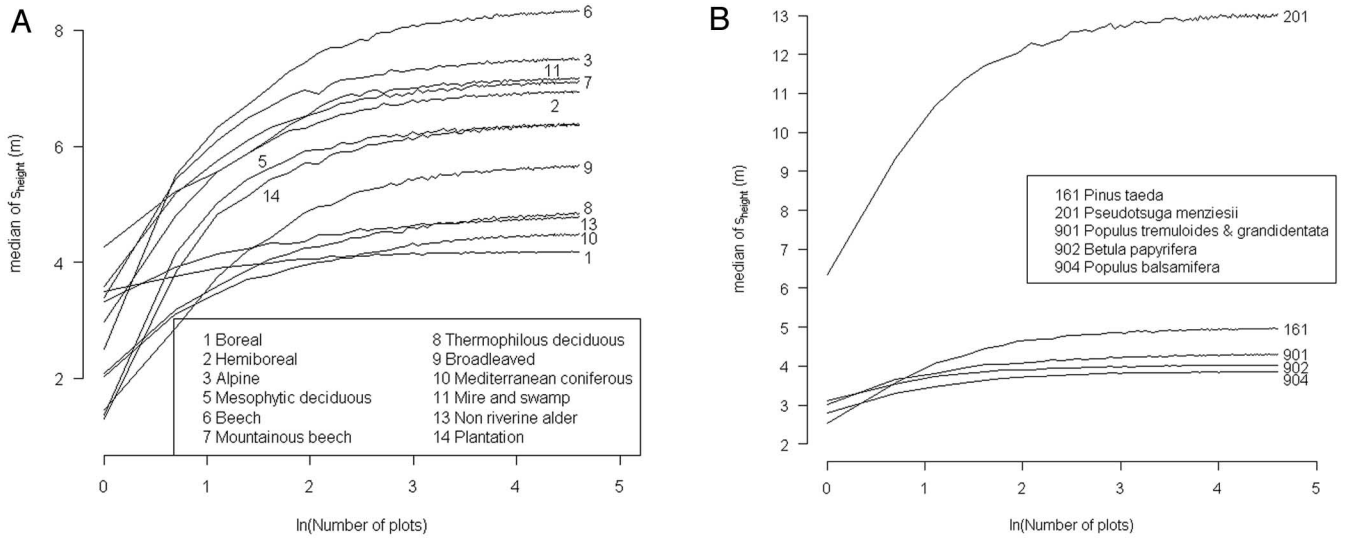

Figure 5. Medians of s_{ht} for European (A) and American (B) forest categories: ln(2) ≈ 8; ln(4) ≈ 55; ln(6) ≈ 400; and ln(3,000) ≈ 8.

median of distributions of estimate of s_{dbh} for Forest category 201 with Douglas-fir and other large tree species growing in temperate rainforests required approximately 20 plots (ln(20) ≈ 3) (Figure 4B), which was similar to the conditions necessary for obtaining precise estimates for European forest categories.

For European forest categories, most curves of medians of distributions of estimates of s_{ht} versus number of plots were steeper than curves of median s_{dbh} versus number of plots (Figures 4A and 5A). The greatest ht diversity was for Beech forest (Forest category 6). For the other European forest categories and the American forest categories, stable estimates of the medians of distributions of estimates of s_{ht} were obtained using approximately 30 plots (ln (30) ≈ 3.5) (Figure 5A and B). However, for the most northern European category, Boreal forest (Forest category 1) and the American deciduous forest categories dominated by pioneer tree species, approximately 5 plots (ln(5) ≈ 1.6) were sufficient for s_{ht} to approach an asymptote for the total numbers of plots for the forest categories. For these forest categories, the diversities of dbh and ht as estimated using our indicators were small.

Spatial Diversity Distribution by Distance Groups

Estimates of s_{dbh} and s_{ht} were maximum for the countries with the greatest separation distance (approximately 8,100 km; ln (8,100) ≈ 9) (Figure 6), but the differences were not statistically significant. However, the variations around the averages were statistically significantly different for different distance groups (Levene's test of homogeneity of variance using both mean and median as center, $P < 0.001$).

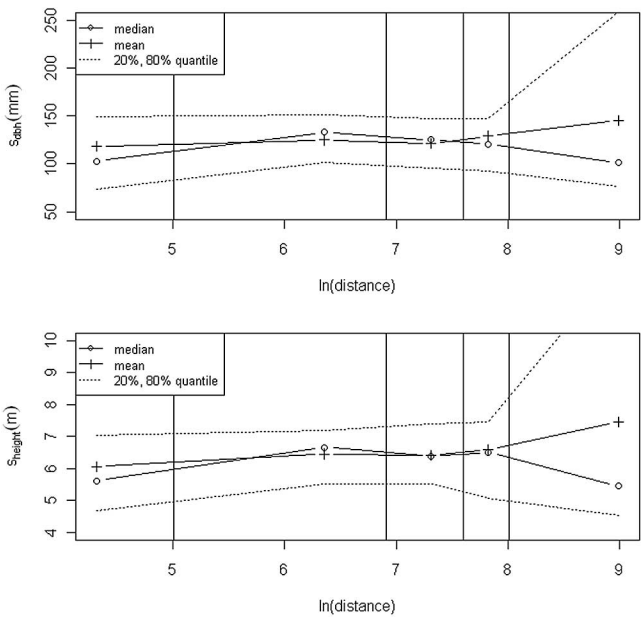

Figure 6. Distance curves for s_{dbh} (top) and s_{ht} (bottom) for five distance groups (1–5) with the breaks of 150, 1,000, 2,000, and 3,000 km (solid vertical lines): ln(150) ≈ 5; ln(400) ≈ 6; ln(1,100) ≈ 7; ln(3,000) ≈ 8; and ln(8,100) ≈ 9.

Further, the medians of the estimates of the diversity indicators decreased for the most distant country groups, which indicated a highly skewed distribution for dbh and ht in the group with regional units separated by distances of more than 3,000 km. This result supports the previous hypothesis that tree ht and dbh are more similar within the European and American regional units than between them.

Discussion

The natural structural heterogeneity of forests depends on the growth conditions of the forest categories which, in turn, depend mainly on climate and soil composition (Breckle 2002). In general, more northern forest categories, such as boreal forests with less favorable growth conditions, have less complex natural structures than categories in southern forests, such as in Mountainous beech forests (Forest category 7) in the temperate zone (see Figures 4 and 5). We were able to illustrate this general diversity gradient with our NFI database using a sample of only 100 randomly chosen plots for the different forest categories. However, regardless of climatic constraints, more heterogeneous forests, even in boreal regions, are richer in habitats and favor the life conditions necessary for forest specialists as opposed to ubiquitous species (Hanski and Hammond 1995, Winter and Möller 2008). Most European temperate forests have been shaped by silvicultural management and are not threatened by deforestation (Foley et al. 2005). However, these forests suffer loss of ecological complexity by simplification to secondary stands and fragmentation (Noss 1990) and are inhabited by increasing numbers of ubiquitous species and decreasing numbers of forest specialists (Duelli and Obrist 2003).

The primary objective of monitoring forest structure is to assess sustainable forest management (Ciancio et al. 1999). To accomplish this objective, NFIs collect scientifically sound and comparable biodiversity information so that estimates of biodiversity indicators can be harmonized. The sensitivity of our proposed indicators to structural changes within forest categories must be tested in the future using large-scale NFI time series of data. Large-scale diversity studies on structural variables that use data from different continents have not been reported in the forestry literature until recently. However, McRoberts et al. (2008) reported a study using data from one of the same American ecoprovinces as was used for this study with approximately the same number of plots although with more than 300,000 trees. McRoberts et al. (2008) showed that mean dbh is highly positively correlated with alpha plot-level diversity and even more positively correlated with gamma diversity ($r = 0.99$). This finding supports our idea to study the uncertainty of gamma diversity estimates in more detail. However, because the ranges between minimum and maximum dbh and ht are constrained by the natural growth potential of tree species, structural diversity can be precisely estimated using a small number of plots for different forest categories and ecoprovinces. On the contrary, however, Winter et al. (2011) used data from the same database used for this study and found that the number of plots in the database was not sufficient to precisely estimate gamma tree species diversity.

For our study, which included a large number of plots and 2,500 iterations for each estimate, we assumed that the consequences of combining data from fixed area plots and relascope data were minor. However, this assumption should be verified.

Further consideration must be given to the results for Plantation (Forest category 14). Because stands in this category are established on sites with quite different growth conditions, there is more potential for greater structural gamma diversity than for natural forest categories. Thus, the results for the Plantation category were not comparable to results for the other 13 forest categories.

However, indicator estimates are recommended to be classified by the proposed subdivisions of the European forest categories (EEA 2006) used for this our study. Thus, our study represents a feasibility test for this MCPFE indicator on large scales. In addition, Spies and Franklin (1991) found s_{dbh} and s_{ht} differences for successional stages of forest stands, whereas we found them for European forest categories (EEA 2006) and American ecoprovinces (Bailey 1976).

Our study focused on the general assessment of uncertainty using subsamples of available NFI data for purposes of reporting gamma structural diversity. However, for future studies, diversity indicators that are sensitive to small changes in NFI time series should be sought. One proposal as a result of our study is to test different SD classes for dbh and ht. Changes in the classes could indicate changes in forest structural composition. Positive changes in large deviation classes could indicate a trend to more heterogeneously structured forests, whereas positive changes in the small deviation classes would indicate a trend to more homogenously structured forests.

Conclusion

Our study on the uncertainty of estimates of gamma forest diversity indicators showed that indicators based on dbh and ht as the most commonly measured NFI structural variables are good candidates for reporting forest biodiversity at large scales for different ecologically based forest categories. Approximately 100 and 150 randomly selected plots from our large database were generally enough to obtain precise estimates of our four indicators of forest structural complexity for different forest categories and at very large geographic scales, respectively. Consequently, for common reporting, subsets of total NFI data sets may be sufficient and may be selected to reduce time-consuming gathering and harmonization of complete NFI country data sets.

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