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Forest structure indicators based on tree size inequality and their relationships to airborne laser scanning

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Academic dissertation

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ABSTRACT

The subject of this doctoral thesis is the non-spatial indices of horizontal differentiation that can be used as indicators of forest structural complexity, specifically as descriptors of tree size inequality. The body of the thesis focuses primarily on the indicators themselves, while the appended articles tackle issues mainly related to their practical estimation using airborne laser scanning (ALS) remote sensing. The overall research is framed in the context of developing a system of indicators that can be applied at pan-European level, whose implementation in practice is foreseen in the advent of national ALS surveying programmes.

A list of indicators available in the scientific literature for describing forest structural heterogeneity by means of horizontal differentiation was tested. Indices based on the theory of information demonstrated critical inconsistencies, which rendered them inadequate for describing tree size inequality. This was revealed using the theory on intrinsic ordering, and illustrated with diversity and equitability profiles. The use of Shannon, and similar indices based on generalized entropy, to describe diversity between size classes, which has been common practice, is therefore discouraged. The link between majorization and Lorenz ordering was established for the specific case of tree size distributions, discussing the reliability of analysing the Lorenz curve to fully describe size inequality in tree populations.

In forest science, the Lorenz curve relates stem frequency distributions to their corresponding basal area-weighted distributions. Indicators based on the Lorenz curve, such as the Gini coefficient (GC), were therefore chosen for their ALS-based estimation. Adding an indicator describing Lorenz curve’s asymmetry was deemed necessary for describing relative understorey development. Research demonstrated the convenience of using the basal area larger than the mean ($BALM$), as it defined the position of the Lorenz curve inflexion point, which depicts the quadratic mean diameter (QMD). It was observed that, when using Lorenz curves to describe forest structure, the position of the QMD should be compared with the Lorenz curve of a theoretical uniform DBH distribution, which represents maximum entropy. Accordingly, this thesis includes a discussion of how Lorenz ordering can be used as a method, providing a scale for simultaneously comparing relative dispersion and entropy.

In conclusion, the final recommended indicators are GC and $BALM$, since this bivariate description of forest structure fully characterises the relationships of relative dominance among trees in a forest population. The most similar neighbour (MSN) imputation of tree lists is defended as a substantially convenient method for predicting these indicators by ALS remote sensing, whereas approaches based on individual tree detection are discouraged.

Keywords: Lorenz curve, Gini coefficient, basal area larger than mean, quadratic mean diameter, Shannon, entropy, intrinsic diversity ordering, horizontal differentiation, pan-European indicators, Lidar, national airborne laser surveying programmes.

PREFACE

This doctoral thesis presents the results and conclusions of research carried out at the European Forest Institute (EFI) headquarters in Joensuu (Finland), based on a personal research proposal originally entitled “Pan-European indicators of forest structural complexity from airborne laser scanning”. The Foundation for European Forest Research (FEFR) awarded a grant from Metsähallitus (Finnish Forest Service) for completing this research during November 2010 – June 2014. The ultimate goal of this research, the development of an objective methodology that can be implemented trans-nationally, cannot be fully accomplished by one researcher alone, however, this doctoral work lays the foundations of an idea that may be feasible in the medium-term, thanks to the current development of national airborne laser surveying programmes. The continuation of research needed to make it a reality has now been assured through a fellowship at the University of Cambridge, granted by a Marie Skłodowska-Curie Action. I would like to raise the awareness of all interested parties that may wish to participate in the practical implementation of a remote sensing-based pan-European indicator scheme in the coming years.

I would like to convey my sincere thanks to my supervisors and other research collaborators for the advice and assistance they provided throughout these years. In 2011, I enrolled as a doctoral candidate at the University of Eastern Finland (UEF), with Prof. Matti Maltamo and Prof. Petteri Packalen as supervisors. In addition to my supervisors, I have a close collaboration with Dr Lauri Mehtätalo, which I wish to maintain in the years to come. I wish to also express my gratitude to the other co-authors of the articles included in this thesis, Prof. Timo Tokola and Dr Jari Vauhkonen from UEF and Dr Kalle Eerikäinen and Mr Juho Pitkänen from LUKE, for the work that they carried out. I express my gratitude to the thesis pre-examiners and article reviewers, especially to Dr Jeffrey Gove (USDA Forest Service), for his constructive comments and ideas, provided during reviewing processes.

Prof. Gert-Jan Nabuurs was my supervisor at EFI during the period he held the position of Assistant Director, after which Prof. Lauri Hetemäki took over. I express my gratitude to all EFI staff who were helpful and friendly during my work. I wish to particularly thank Dr Risto Päivinen, Dr Marcus Lindner, Dr Johannes Verkerk, Dr Diana Tuomasjukka and Ms Leena Salminen. I am especially thankful that collaborating with EFI and UEF staff also allowed me to participate in other international research projects which, although they delayed the presentation of this doctoral thesis, enriched my professional experience. During this period I also supervised students in the completion of their Master’s theses, Mr Marc Caufapé, Mr Javier Cuesta and Mr Alejandro Matos, whom I would also like to thank for their work and interest.

I also want to give a special mention to my former collaborators at the Technical University of Madrid, without whom none of my accomplishments would ever have taken place. Among others: Prof. José Antonio Manzanera, Dr Antonio García-Abril, Dr Susana Martin-Fernández and Dr Cristina Pascual. The research carried out during this doctoral thesis is grounded on their goal of promoting sustainable forest management, and their long-term research in the forests of Valsaín have undoubtedly made these findings possible.

In addition to the FEFR grant, funding was also provided by the Graduate School of Forest Sciences (GSForest) and the Finnish Society of Forest Sciences. This funding allowed the presentation of results at the ForestSAT, Silvilaser and EFINORD-SNS conference series. Studies II and III were presented in special issues organised by those conferences.

Joensuu, April 2015

LIST OF ORIGINAL ARTICLES

This thesis is supported by the following articles, referred to according to Roman numerals. They are reprinted with kind permission of the publishers. The body of the thesis summarises the overall objectives and methodology employed. It also includes original results about forest structure indicators not published elsewhere. This thesis is therefore meant to be read along with the articles, which mainly tackle the remote sensing estimation and application of indicators. The overall work is structured in three main parts: forest indicators (thesis body and Study I), remote sensing estimation (Studies II-IV) and applications of the developed methodology (Studies V-VI).

I. Valbuena R., Packalen P., Martín-Fernández S., Maltamo M. (2012) Diversity and equitability ordering profiles applied to the study of forest structure. *Forest Ecology and Management* 276: 185–195. http://dx.doi.org/10.1016/j.foreco.2012.03.036

II. Valbuena R., Maltamo M., Martín-Fernández S., Packalen P., Pascual C. Nabuurs G.J. (2013) Patterns of covariance between airborne laser scanning metrics and Lorenz curve descriptors of tree size inequality. *Canadian Journal of Remote Sensing* 39(S1): S18–S31. http://dx.doi.org/10.5589/m13-012

III. Valbuena R., Packalen P., Tokola T., Maltamo M. (2014) Canonical correlation analysis for interpreting airborne laser scanning metrics along the Lorenz curve of tree size inequality. *Baltic Forestry* 20(2): 326–332. http://www.balticforestry.mi.lt. [Cited 29 April 2015].

IV. Valbuena R., Vauhkonen J., Packalen P., Pitkänen J., Maltamo M. (2014) Comparison of airborne laser scanning methods for estimating forest structure indicators based on Lorenz curves. *ISPRS Journal of Photogrammetry & Remote Sensing* 95: 23–33. http://dx.doi.org/10.1016/j.isprsjprs.2014.06.002

V. Valbuena R., Packalen P., García-Abril A., Mehtätalo L., Maltamo M. (2013) Characterizing forest structural types and shelterwood dynamics from Lorenz-based indicators predicted by airborne laser scanning. *Canadian Journal of Forest Research* 43(11): 1063–1074. http://dx.doi.org/10.1139/cjfr-2013-0147

VI. Valbuena R., Eerikäinen K., Packalen P., Maltamo M. (2016) Gini coefficient predictions from airborne lidar remote sensing display the effect of management intensity on forest structure. *Ecological Indicators* 60: 574–585. http://dx.doi.org/10.1016/j.ecolind.2015.08.001

Rubén Valbuena was responsible for all calculations and analyses, except for individual tree detection methods in Article IV, which were carried out by Dr Jari Vauhkonen and Mr. Juho Pitkänen. He participated in field data collection in Valsaín (Studies I, II and V) during earlier work at the Technical University of Madrid. Field data for Koli (Study V) was kindly provided by the Finnish Natural Resources Institute (LUKE) and UEF, which also supplied data for Kiihtelysvaara (Studies III, IV and V). Research in Studies I–III and V was based solely on the original ideas of Rubén Valbuena, whereas the research lines for Studies IV and VI were developed jointly by their corresponding co-authors. All co-authors contributed at various stages of the analyses and writing, improving the quality of the final articles.

TABLE OF CONTENTS

GLOSSARY OF ABBREVIATIONS

ABA	Area-based approach for ALS estimation, which refers to the computation of metrics from the height distributions of ALS returns extracted over an area and their use as auxiliary variables in the estimation of forest parameters.
a.s.l.	Above sea level
AIC	Akaike information criterion
ALS	Airborne laser scanning. A type of lidar remote sensing technique consisting of a laser system with scanning capability carried from an airborne vehicle.
$BALM$	Basal area (in proportion) larger than mean (QMD)
CCA	Canonical correlation analysis
CHM	Canopy height model
CV	Coefficient of variation
DBH	Diameter at breast height
DTM	Digital terrain model
FST	Forest structural type
GC	Gini coefficient
ITD	Individual tree detection
LA	Lorenz asymmetry
LARS	Least angle regression
LASSO	Least absolute shrinkage and selection operator
Lidar	Blend of “light” and “radar”, which refers to a detection system which works on the principle of radar, but uses light from a laser. It is customarily assumed to be an acronym standing for either “light detection and ranging” or “laser imaging, detection and ranging”
MCPFE	Ministerial Conference for the Protection of Forest in Europe
MMI	Multi-model inference
MSN	Most similar neighbour. A method for NN imputation based on CCA.
NASP	National ALS surveying programmes
NN	Nearest neighbour
$NSLM$	Number of stems (in proportion) larger than mean (QMD)
PLS	Partial least squares
PRESS	Predicted sum of squares
QMD	Quadratic mean diameter
RF	Random forest
RMSE	Root mean squared error
SS	Sum of squares
USDA	US Department of Agriculture

See also the summary of ALS metrics provided as an appendix.

A note about notation consistency

Ensuring consistency in notation during the work carried out for this doctoral thesis has been a challenge, because this research linked the works of various authors, apparently unconnected, which had not been related previously. Study I showed the link between majorization and Lorenz ordering (see Eqs. 1-3 below). This has been well studied in mathematics, although Study I was the first to apply it to the specific case of describing tree size distributions. Nomenclature employed by Liu et al. (2007) was then adopted, as it provided a common framework for all intrinsic ordering methods. For this reason, the original notation for majorization $M_r(x_r)$ was passed on to Studies II-V when referring to the Lorenz curve – instead of the more customary $L(u)$ –. When analysing the convenience of using Damgaard and Weiner's (2000) asymmetry coefficient for the Lorenz curve (originally $S = F(\hat{\mu}) + L(\hat{\mu})$), Study II first observed that these components match the values of the curve corresponding to the average basal area (Study II: Eq. 4). The diameter which corresponds to the mean basal area is the quadratic mean diameter (denoted as D_g in Study II, but as QMD in the remainder, see Curtis and Marshall (2000)). For this reason, in Study V the notation for $L(\hat{\mu})$ was substituted by $M(x_{QMD})$, and $F(\hat{\mu})$ by x_{QMD}; while Lorenz asymmetry was denoted as LA (and transformed to be the average of its components, see Study V: 1067). It was then realised that the concept of the cumulated relative proportion of basal area above the QMD was an idea already employed in forest management by Gove (2004), who used the term '$BALM$' as an acronym for "basal area larger than mean"[1,2]. It was then decided to use this terminology thereafter, in Study IV, and $M(x_{QMD})$ was substituted by $BALM$, and x_{QMD} was denominated $NSLM$, which stands for "number of stems larger than mean", for simplicity. $NSLM$ and $BALM$ (Gove 2004) therefore represent the values of x and y-axes for a concave Lorenz curve inflexion point, as explained for $F(\hat{\mu})$ and $L(\hat{\mu})$ in Damgaard and Weiner (2000). I understand that this inconsistency in nomenclature across articles can make the logic used hard to follow. For this reason, internal consistency has been assured for the body of this thesis, and this table helps in interpreting the differing notation employed in the individual articles:

Table of nomenclature correspondences across articles.

Variable	Damgaard and Weiner (2000)	Study II	Studies III and V	Study IV and Gove (2004)
Quadratic mean diameter	-	D_g	QMD	QMD
Lorenz asymmetry	S	S	LA	LA
Basal area larger than mean	$L(\hat{\mu})$	$M_{\bar{g}}$	$M(x_{QMD})$	$BALM$
Number of stems larger than mean	$F(\hat{\mu})$	$x_{\bar{g}}$	x_{QMD}	$NSLM$

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[1] As defined by Gove (2004), "mean" refers to the arithmetic mean of the basal area which, in turn, is equivalent to the quadratic mean of the diameter. $BALM$ can therefore be referred to as either "basal area larger than mean" or "basal area larger than quadratic mean diameter", and both are correct.

[2] Section 3.2.4 further comments on the relationship of $BALM$ (a population parameter) to BAL_i, an individual tree index of competition (Wykoff 1990; Vanclay 1994).

ERRATA & CORRIGENDA

Study I

On page 188, the definition of reverse J states: "*In stands undergoing seed regeneration, samplings co-exist with the dominant canopy*"; where it should be: "*In stands undergoing seed regeneration, saplings coexist with the dominant canopy*".

On page 189, there is a small erratum, as it should simply say "*becoming less weighted towards (a) for the entropy measures of higher order*".

On page 194, while drawing conclusions about the interpretation of Lorenz curve of tree sizes, it was stated that: "*for forest plots obtaining $GC > 0.5$, starting from a peaked reverse J (FST IVa), the success of natural regeneration and ingrowth can be indicated by decreasing GCs. Also, the asymmetry coefficient would shift from $S < 1$ to $S > 1$ (for concave Lorenz curves, but from $S > 1$ to $S < 1$ for convex ones) as an indication of achieved recruitment (FST III) from a reverse J (FST IVb)*". In this paper this was hypothesised according to the mathematical properties observed in the index of Lorenz asymmetry (S). The empirical Lorenz curves later observed during Study V, however, demonstrated that S displayed the opposite evolution during ingrowth (Article V: Fig. 4). Lorenz asymmetry is directly related to the skewness of the diameter distribution and changes in S would be determined by the dynamics of each type of forest ecosystem or management regime. The value of S therefore depends on whether ingrowth in the understory develops into a single uniform cohort (leading to a bimodal distribution) or in a more irregular manner. In the former case, referring to the comparison between a bimodal and a reverse J distribution, it should instead be explained that the basal area-weighted distribution develops from being negatively skewed (to the right) toward becoming positively skewed (to the left), and so do their Lorenz curves (if concave, i.e. that obtained when ranking trees in decreasing order). That sentence should thus be corrected into: "*the asymmetry coefficient would shift from $S > 1$ to $S < 1$ (for concave Lorenz curves, but from $S < 1$ to $S > 1$ for convex ones) as an indication of achieved recruitment (FST III) from a reverse J (FST IVb)*". This error was partially amended in Study V: "*The development of uneven-sized patches at gaps opened by forest disturbances at even-sized stands was therefore indicated by $LA \geq 0.5$, later becoming $LA < 0.5$ once ingrowth succeeded*" (page 1069); note that $LA = S/2$.

Study II

On page S21, there is a sentence explaining the relationship between GC and the L-moments, which states: "*GC is the second L-moment (Hosking 1990), as it estimates dispersion relative to average (concentration), therefore isolating the description of dbh-inequality from the development stage and D_g of a given plot*". Although it is true that GC describes concentration, this statement is partly mistaken, as GC corresponds to the ratio between the second and first moments, a.k.a. the L-coefficient of variation. This error was corrected in subsequent articles: Study III "*The GC is the ratio between the second and first L-moments, and it is therefore often referred to as L-coefficient of variation (L.CV; Hosking 1990)*" (page 326), and Study IV "*The GC is the ratio between the second and first L-moments, and therefore a second order descriptor of concentration, i.e. relative dispersion (Hosking 1990)*" (page 24).

1 INTRODUCTION

1.1 Background and Motivation

1.1.1 Definition of Forest Structural Complexity

Forests are typically described using stand parameters, and ecosystems by species diversity (Franklin et al. 2002). These attributes can be used to describe essential ecological processes and habitat characteristics: natural disturbance, forest succession, competition, etc. (Spies 1998). Due to size variation, traditional descriptions of species diversity does not suffice for a full understanding of the structural complexity of forest habitats (Lähde et al. 1999b). The structural complexity of forests therefore has multiple dimensions (McElhinny et al. 2005):

- *Structure*: the spatial arrangement of the various components of the ecosystem. The indicators referred to in the present doctoral thesis mainly describe this dimension of forest structural complexity, using airborne laser scanning (ALS).
- *Composition*: the identity and variety of ecosystem components; for instance, species richness and abundances. Although remote sensing also has potential in this dimension (Simonson et al. 2012), it is out of the scope of this doctoral thesis.
- *Function*: the ecological processes involved in a forest population, such as rates of different processes involved in the cycling of nutrients, species interaction, etc. There are many studies on the possibilities of assessing properties of this kind, such as symmetric (Pedersen et al. 2012) and asymmetric competition (Kellner and Asner 2009).

Structural complexity of forest is therefore fully accounted for only when all these dimension are described (Spies 1998). Composition, structure and function are often interdependent (McElhinny et al. 2005; Gao et al. 2014). For this reason, they are not exclusive, and forest attributes do not clearly describe one single category. Instead, all these components are described simultaneously in structural attributes.

1.1.2 Importance of indicators of forest structural complexity and forest structural types (FSTs) in the provision of ecosystem services

The structure of forests is key in determining many ecosystem functions (MacArthur and MacArthur 1961), since the distribution of forests patches and their dynamics are important because they regulate habitat structure, wildlife distribution, and determine the delivery of ecosystem services such as biodiversity, erosion control, water availability and carbon storage. It is essential to involve forest structure indicators in management for sustainable forest use (Gove et al. 1994). Alterations in forest structure are a critical driver of change in carbon stocks and evapotranspiration. Tree diameter distribution affects species diversity (Spies and Franklin 1991), for instance by ensuring a continuous supply of dead trees (Poage and Tappeiner 2005) or providing habitat quality for fauna (Willson 1974; Erdelen 1984). For these reasons, the Ministerial Conference for the Protection of Forest in Europe (FOREST EUROPE; formerly MCPFE) reported the importance of measuring diameter distribution by area and forest type (MCPFE 2003: Indicator 1.3; Ståhl et al. 2011). Indicators and classifications of forest structural complexity can provide concise descriptors that could be practical for ecological assessment and monitoring (Gao et al. 2014; Bosela et al. 2016). For this reason, technologies to estimate structural complexity indicators can be used for ecological evaluation, to assist in forest management planning, or for choosing the most favourable recreational uses (Pretzsch 2011; Ståhl et al. 2011).

1.1.3 Using remote sensing and forest structure assessment for supporting the increasing complexity of forest management systems

The provision of objective means for assessing and monitoring the effects of management practices in forest structure is one of the most important motivations for developing an objective system that can be used for trans-national comparison. In general, it can be stated that Europe is currently undergoing a shift in forest management strategies from plantation monocultures toward more environmental-friendly systems (Nabuurs et al. 2007) such as continuous cover forestry (Schütz et al. 2012; Puettmann et al. 2015). But there is a very difficult question to address: which management system is more favourable in terms of maintaining the diversity of our forest and at the same time maintaining a sustainable use of raw materials? What science can tell us is that both management systems have their own benefits and assets. Consequently, the best choice is to remain flexible and avoid general policies and guidelines for prescribing the same silvicultural regime in every single case (Bunnell and Huggard 1999). Biodiversity is enhanced by increasing complexity of forest structure which, in turn, is better kept through a diversity of management systems across landscapes (Rendon et al. 2014). This hetereogeneity at landscape level cannot be reliably evaluated by sampling forest areas sparsely, and therefore the role of remote sensing in providing data for biodiversity conservation is an obvious option for improvement (Marvin et al. 2014). There is an opportunity to use the detailed information provided by ALS and apply it to more complex management systems that change over space and time (Packalén et al. 2011). Indicators extracted from ALS at a trans-national scale (e.g. pan-European) can therefore assist in further answering these scientific questions, as well as monitoring the effects that management has on forest health and biodiversity.

Advantages and disadvantages of even-aged and uneven-aged forest management

Many authors have studied the advantages and disadvantages of even-aged and uneven-aged forest management, which include both economic and ecological aspects among others (Jactel et al. 2012). It may be assumed that even-aged management would in principle be more profitable, by maximising net present value with fixed rotation periods of thinning and clear-cutting. On the other hand, in the absence of human intervention, forest dynamics seem to naturally lead to an age distribution resembling a reversed J (Hett and Loucks 1976; Aber 1979; Lähde et al. 1991), which can be followed by regeneration or a terminal phase (Oliver and Larson 1996; Franklin et al. 2002; Coomes and Allen 2007; Huber 2011). Using uneven-aged management can be assumed to provide a number of environmental assets (Ferris-Kaan et al. 1998; Solomon and Gove 1999), however, a number of arguments may be found that reach opposing conclusions, and the remote sensing-assisted assessment of forest structure can provide good insights towards answering these questions.

The economic value of uneven-sized stands can be optimised through a proper choice of selective cutting cycles (Buongiorno et al. 1994), and thus uneven-aged management can be more profitable than even-aged rotation forestry (Pukkala et al. 2010). On the other hand, creating gaps in a uniform canopy may affect wood quality negatively (MacDonald et al. 2010). There are also many environmental benefits that can be argued in favour of either option, as well as those with regards to recreational (Lehtonen et al. 2003) and multifunctional uses of forests (Pukkala et al. 2011). The presence of various strata in forest canopies provides habitat quality for fauna (Willson 1974). It can be argued, however, that continuous cover forestry can inhibit the natural regeneration of shade-intolerant species (Appelroth 1948 – as cited in Laiho et al. 2011 –). Continuous cover forestry is also criticised for encouraging inbreeding between overlapping generations in species with limited pollen dispersal, thus affecting genetic diversity (Finkeldey and Ziehe 2004). Management regimes based on clear-cut rotations lead to landscape fragmentation, affecting biodiversity, scenic values, and enhancing soil loss and risk of erosion. For this reason, uneven-aged management has been defended for favouring forest resilience against climate change (Lafond et al. 2013). Moreover, while both even and uneven-sized stands are suited for recreational uses and appreciated for their beauty, clear-cuts are usually disliked (Rydberg and Falck 2000). Complex forest structures can also be seen as an impediment to certain recreational uses such as hiking or hunting (Gundersen and Frivold 2008). Recreationists also like diversity at landscape scale, and thus open spots, in clear cut situations are quite often valued positively. It is the ’mess’ right after a clearcut that is regarded negatively. Berry or mushroom-picking can be another recreational criteria, as bilberry production is improved in shadowy conditions (Ihalainen et al. 2002), and can be maintained by management assuring balanced forest structures (Laiho et al. 2011).

Disaster risk assessment is another important issue for which the availability of reliable information on stand structure may be of key importance. It can be used to evaluate forest fuel types and the risk of uncontrolled wild fires (González-Olabarria et al. 2005), or to prevent storm damage (Gardiner et al. 2005; Andersson et al. 2014). Concerning the use of forests as carbon sinks, it seems unclear whether even or uneven-management would be more beneficial with regards to carbon sequestration (Pukkala et al. 2011). These are just some reasons why a forest manager may benefit from having good information on the structural complexity of different areas of a forest, which can be used in a multi-criteria decision analysis. Direct estimation of these indices by means of ALS data may provide useful information not only for multi-temporal and spatial comparison, but also for automatic stand delineation, stratification into forest types, or decision making in forest management (Packalén et al. 2011).

The group shelterwood management system

In the context of silvicultural systems leading to continuous cover and uneven-sized forest structures, I will shortly introduce the shelterwood system, as it was one of the applications of the methods developed in this doctoral thesis. This type of management was chosen as it leads to a wide range forest structural types, which may even co-exist within a relatively small area when applied in a patchy manner (group selection). Although it leads to zones of uneven-sized forest structures, the shelterwood method is essentially an even-aged silvicultural system, as it consists of promoting the establishment of a new even-aged cohort which develops under the shelter and protection of the old one, which is removed gradually in a series of fellings (Fig. 1). The idea is similar to the seed-tree system but on a different spatio-temporal scale, as similar treatments are more gradually applied over smaller management units. This way, the above-mentioned problem of inhibiting the natural regeneration of shade-intolerant species is overcome, satisfying requirements for the sustainable exploitation of the forest resource (Laiho et al. 2011) while preserving the continuous cover, the complexity of its structure, and other ecosystem services (Lähde et al. 1999b).

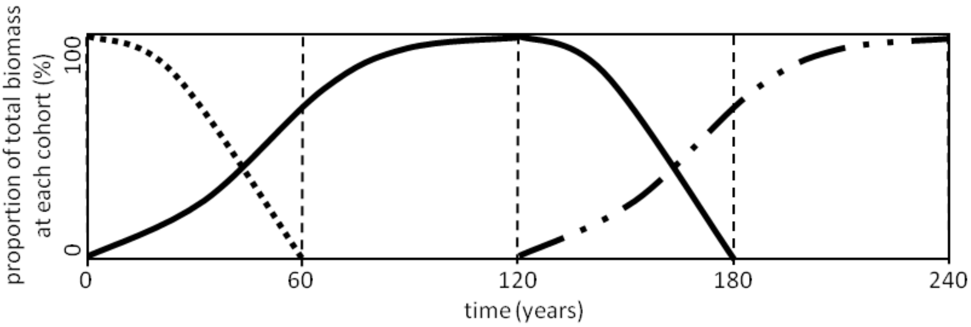

Figure 1. Diagram representing the rotation period of the shelterwood management system. The evolution of the relative biomass or timber volume in each cohort is compared along a two-period range of time (240 years). When the previous dominant cohort (dotted line) starts to decay, the natural regeneration of a new cohort (solid line) starts in the understory. Uneven-sized forest structural types (FST; Study V: Figs. 1.d-f) are thus found in the first half of the period (0-60 years). This same cohort later becomes dominant, reaching the stem exclusion stage and inhibiting shade-intolerant regeneration. Even-sized structures are therefore common (Study V: Figs. 1.a-b) during the second half of the period (60-120 years). Opening gaps in the dominant canopy allows the re-initiation of the next cohort (Study V: Fig. 1c) and the start of the next period in the 120 years (dot-dashed line). The outcome is a great variety of forest structural types co-existing in the same forest stand. Courtesy: Antonio García Abril (Technical University of Madrid; adapted from Velarde et al. 2014: Fig.44).

The implementation of a shelterwood system in patches faces, however, two main challenges to the practical management of the forest. Firstly, the optimization method is more difficult to develop when trees of different ages share the same forest area and compete with one another (Gove et al. 1995; O'Hara et al. 2004). Secondly, it requires a system for inventorying the whole forest area, and monitoring it at higher frequency, since within-stand complexity requires the means for detecting forest areas in need of specific treatments. Remote sensing provides an opportunity to develop management systems able to deal with this increasing complexity (Packalén et al. 2011). The information obtained in remote sensing should be translated into concise indicators that can allow objective diagnosis and comparison.

1.2 Evaluating the structural complexity of forests

There have been several attempts to quantitatively describe the structural complexity of forests by means of simple indicators (Neumann and Starlinger 2001; Motz et al. 2010). Pommerening (2002) provides an overview of them all, and their general classification into non-spatial and spatial (neighbourhood) indices, and also distinguishes between those measuring the spatial distribution of stems, species mixture, or variations in tree dimensions and biomass distribution in both horizontal and vertical strata. The different attributes of structural complexity that can be explained from a given forest (Section 1.1.1) could be grouped into these categories (adapted from McElhinny et al. 2005):

1. *Abundance*. These are common stand parameters: density, basal area, mean diameter, dominant height, volume, biomass, etc. The estimation of these type of properties is well settled in operational ALS inventory (Næsset et al. 2004; Maltamo et al. 2014). They can also be aimed at a given attribute or element of the forest population, such as large trees or coarse woody debris.

2. *Horizontal structure.* These are spatially-explicit indicators describing the positional distribution of elements in the population, such as neighbouring analysis (Pommerening 2002). They are typically based on point process and second order statistics, which analyse spatial patterns and model the variability of tree positions. Besides of the spatial positions, they can include additional attributes: such as species or sizes (which, in this context, are called *marks*). There is a wide range of indicators in this group, but they are out of the scope of the present doctoral thesis, although they are useful and can also be estimated from ALS remote sensing (Packalén et al. 2013).
3. *Differentiation.* Includes all sorts of indicators describing the relative dimensions of neighbouring trees, but not taking into account their relative locations (i.e. considering the marks only). They are thus non-spatially explicit indicators comparing relative amounts and proportions of target elements in a population, and their variation. We can distinguish *horizontal differentiation*, when indicators are based on tree diameters at breast height (DBH), and *vertical differentiation* when using heights (sensu Kint et al. 2000). They compare to those of horizontal structure in that only the variation in the marks is accounted for, and therefore a random distribution of elements is often assumed. This doctoral thesis focuses on these type of indicators, measured from tree DBH (horizontal differentiation). These type of indicators may be measures of forest attributes describing either:
    3.1. *Richness.* This is the number of different elements (species, layers, DBH classes, etc.) constituting a tree assemblage. For instance, Maltamo et al. (1997) and Ståhl et al. (2011) described forest structure as the number of existing tree layers. While richness is defined by the different types of elements present in the population, relative abundances (see below) describe their quantities.
    3.2. *Equitability.* Describes the relative proportions of these elements, constituting the population. In essence, this is the concept of *relative abundances* (sensu McElhinny et al. 2005), which is commonly referred to as *evenness* in the case of elements distinguished in the population being categorical (e.g. species). Among those commonly used to describe forest structure many are based on the theory of information (Legendre and Legendre 2012). Indices of equitability are commonly calculated by subtracting the richness component of diversity (e.g. Buongiorno et al. 1994). I would still distinguish three groups of indicators that could, in my opinion, be included within the definition of those providing a concise measure for a distribution of relative abundances:
        3.2.1. *Homogeneity (size variation).* These are dispersion estimates of DBH, height, etc. Examples include the standard deviation of DBH (Spies and Franklin 1991), their coefficient of variation (CV; Coomes and Allen 2007), range (Uuttera et al. 1997) or the Gini coefficient (GC; Weiner 1985). When describing forest structure, some authors have suggested comparing the dispersion of the given variable against a uniform distribution (de Camino 1976; Staudhammer and LeMay 2001) which, in my opinion, is an advantageous approach (see page 49). Although McElhinny et al. (2005) included these as a separate group, they can be seen as measures of relative abundance in a special case when the elements are compared using a continuous ordinal variable (e.g. DBH). Considering these attributes a special case of equitability, I prefer allude to them as descriptors of *size inequality*.

3.2.2. *Dominance or rarity.* As this is the same concept as equitability, these terms are employed if it is important to emphasise when a few of the elements in the population constitute either the most (dominance) or least (rarity) of the overall abundance. I see that including this group is important, as these indicators can help to describe processes related to asymmetric competition. Gove et al. (1994) draw the attention to the concept of rarity in forest structure characterisation. In my own view, measures of skewness (Knox et al. 1989) and kurtosis may be also be included within this group, as they also describe whether there is a large disproportion in the distribution of relative abundances among the elements considered (they would be a special case of dominance for continuous variables).

3.2.3. *Diversity (entropy).* Based on the theory of information, indicators of diversity are also fairly popular, as they provide a concise description of all the above-mention properties of vertical structure in one single measurement. They are most commonly employed to describe diversity among species, however, there have also been many approaches using DBH, height, etc. to describe forest structure, such as foliage height diversity (FHD) (MacArthur and MacArthur 1961), or diameter at breast height (DBH) diversity (e.g. O'Hara et al. 2007; Lexerød and Eid 2006; von Gadow et al. 2012).

In another review article, del Río et al. (2003) suggested that analyses of forest structural complexity can be either static or dynamic. They pointed out the following as approaches to studying dynamics: (1) analysis of plots located in different areas along the full chronosequence of the forest development cycle; (2) using permanent plots (Solomon and Gove 1999; Sullivan et al. 2001; Pretzsch et al. 2014); or (3) modelling approaches (Frelich et al. 1998). Structural complexity can also be analysed at higher levels as delta (landscape) or beta (mesohabitat) diversity and equitability, inter-stand heterogeneity, whereas alpha measures are performed at a finer within-stand scale (Whittaker 1977). Indices based on the theory of information and the concept of diversity are popular, and so most authors speak of *structural diversity* (Neumann and Starlinger 2001) when using indicators within the group which I denominated above as indices of tree size differentiation. McElhinny et al. (2005) prefer to use the boarded term *structural complexity* to express all the dimensions involved in forest ecosystems, and I agree (see Section 3.1).

1.2.1 Non-spatial indicators of structural diversity and tree size inequality.

Diversity measures are usually intended to describe species richness and abundance (Magurran 2004). Richness is commonly described by the number of species, and abundance by the number of individuals per species. When measuring structural diversity, richness can be described by the number of DBH or height classes, whereas abundance may be the basal area, volume or biomass per class (Lexerød and Eid 2006). These variables are strongly influenced by larger trees, so that they are preferred to the number of trees since the results are more important regarding forest management (Solomon and Gove 1999). In other words, a reverse J-shaped frequency distribution, which would presumably produce low values of diversity, shows uniformly distributed basal areas between DBH classes, yielding high values in diversity indices, more fairly expressing its complexity. Using basal area, volume or biomass would also be beneficial from a remote sensing perspective, since estimations of basal area and volume by means of ALS are usually more accurate than those obtained for number of stems (Næsset et al. 2004).

This doctoral thesis pertains to the ALS estimation of non-spatial indices of alpha (plot scale) diversity and equitability between DBH classes and tree DBH differentiation. Relative abundances were considered both in terms of number of stems (unweighted) and their basal area (weighted). The reason for disregarding height, volume and biomass was that these are variables usually estimated by allometry, and only rarely directly measured, meaning that model uncertainty was a potential problem in the relationships observed. An initial screening of results showed none significantly different from those obtained by basal areas observed over DBH classes (see page 50). The course of the research will demonstrate that this was a very convenient approach, as the quadratic relationship between the DBH distribution and its area-based weighted counterpart yields a number of desirable mathematical properties (Gove 2003; Curtis and Marshall 2000), from which this research benefited. To avoid inter-specific variation, which may introduce confusion in the properties researched, the forest areas involved in this research were mainly monospecific coniferous stands. Three types of approaches can be found in the literature regarding to the calculation of indices with the noted characteristics:

1) Adaptations of richness, diversity and equitability indices based on the probability of inter-specific encounters (Shannon, Simpson, etc.) to the study of diversity of size classes (Lexerød and Eid 2006);
2) Applying Lorenz ordering to the study of tree size homogeneity (de Camino 1976);
3) Analysing structural complexity based on measures of the dispersion of DBH distributions, such as variance (Staudhammer and LeMay 2001), and or indices describing their shape, such as skewness (Knox et al. 1989).
4) Using theoretical models, such as Weibull distribution functions, and parameter estimation methods (e.g., Gove and Patil 1998; Coomes and Allen 2007).

Table 1 summarises the adaptation of the indices that was initially considered for this research. Most of these indices are widely used to describe diversity of species, and thus their use for studying the structural diversity of forests requires a proper interpretation of the results. Even-sized stands would obtain high values of indices measuring dominance, whereas pluri-stratified forests would indicate higher values of indices influenced by richness. What it is understood as abundance in studies of species diversity would refer to stand density in this study, or relative density between diameter classes. For this reason, a measurement of evenness (equitability) would determine whether or not all classes are equally represented in even-sized forests.

Although most of these indicators simultaneously describe many of the noted structural attributes, each of them is more weighted toward a given property: richness, dominance, diversity, equitability or homogeneity. Indices describing richness are the Margalef (D_{Mg}) and Menhinick (D_{Mn}) indices. Berger–Parker (D_{BP}) is usually described as a dominance index, whereas Simpson (D_{Si}) and McIntosh (D_{MI}) are commonly considered diversity indices. Diversity is a joint measurement of both richness and equitability (Magurran 2004), and perhaps the reason the Shannon index (H') is the most popular may be because it is more weighted towards richness (in other words, the value of the Shannon index is higher for richer populations than for even ones). For this reason, all these diversity indices also have an equitability counterpart: the Shannon (J') Simpson ($E_{1/D}$), and McIntosh (E_{MI}) evenness indices. As they describe equitability alone, they have provided some of the most successful results in describing structural complexity (Buongiorno et al. 1994; Lexerød and Eid 2006). All these indices are essentially based on the theory of information (Legendre and Legendre 2012).

Table 1. Summary of indices initially proposed for the present study, based on literature (adapted from Lexerød and Eid 2006). Formulae are index adaptations to the study of structural diversity of diameter at breast height (DBH) classes. S: number of diameter classes; i,j: size class ranging $1,\dots,S$; N: total number of trees; k: rank (by DBH) of a tree ranging $1,\dots,N$; G: total basal area ($\mathrm{m^2ha^{-1}}$); g_i: basal area in size class i; g_k: basal area for tree with rank k; $g_{\max}$: basal area of the largest size class. Similar adaptations can also be obtained by substituting basal areas by volume (v_i/V) or above-ground biomass (agb_i/AGB), or simply stems number (n_i/N; i.e. unweighted). DHB classes may also be substituted by height classes.

Index	Formula	Range	References
Margalef index	$D_{Mg} = (S-1)/\ln G$	[0,∞]	Clifford and Stephenson (1975); Lexerød and Eid (2006)
Menhinick index	$D_{Mn} = S/\sqrt{G}$	[0,∞]	Whittaker (1977)
Berger–Parker index	$D_{BP} = g_{\max}/G$	[0,1]	Berger and Parker (1970); Lexerød and Eid (2006)
Simpson index	$D_{Si} = \sum_{i=1}^{S}\left(\frac{g_i}{G}\right)^2$	[0,1]	Simpson (1949); Gove et al. (1994); Lexerød and Eid (2006)
Simpson eveness	$E_{1/D} = \frac{1/(1-D_{Si})}{S}$	[0,1]	Smith and Wilson (1996)
Shannon index	$H' = -\sum_{i=1}^{S}\left(\frac{g_i}{G}\right)\ln\left(\frac{g_i}{G}\right)$	[0,ln$S$]	Shannon (1948); MacArthur and MacArthur (1961)[H]; Murdoch et al. (1972)[N,E]; Harper et al. (2003); Rouvinen and Kuuluvainen (2005); O'Hara et al. (2007)[N]; McRoberts et al. (2008)[N]; Lei et al. (2009)[H]; Pretzsch (2011)[N]; von Gadow et al. (2012)
Shannon eveness	$J' = H'/\ln S$	[0,1]	Heip (1974); Buongiorno et al. (1994)[N,E]; Neumann and Starlinger (2001)[H]; O'Hara et al. (2007)[N] Pretzsch (2011)[N]
McIntosh index	$D_{MI} = -\frac{G-\sqrt{\sum_{i=1}^{S} g_i^2}}{G-\sqrt{G}}$	[−∞,∞]	McIntosh (1967); Lexerød and Eid (2006)
McIntosh evenness	$E_{MI} = \frac{G-\sqrt{\sum_{i=1}^{S} g_i^2}}{G-G\sqrt{S}}$	[0,1]	Pielou (1966) ; Lexerød and Eid (2006)
Gini coefficient	$GC = \frac{\sum_{i=1}^{N}\sum_{j=1}^{N}\lvert g_i - g_j\rvert}{2n^2\bar{g}}$	[0,1]	Gini (1921); Weiner and Solbrig (1984)[V]; Knox et al. (1989)[V]; Lei et al. (2009)[H]; Duduman (2011)
de Camino homogeneity	$CH = \frac{\sum_{k=1}^{N}(n_{\le k}/N)}{\sum_{k=1}^{N}[(n_{\le k}/N)-(g_{\le k}/G)]}$	[0,∞]	de Camino (1976)[V]; Bachofen and Zingg (2001)[V]
Structure index based on variance	$s_{DBH}^2 = \sum_{i=1}^{S}\left(\frac{g_i}{G}\right)(DBH_i - \overline{DBH})^2$	[0,1]	Staudhammer and LeMay (2001) (index compares this variance formula with theoretical ones)

[H] these authors (also) considered height classes.

[N] these authors employed the number of individuals within each class (unweighted).

[V] these authors employed volume or biomass instead of basal areas.

[E] some authors also employ an empirical approach to determine the maximum value of diversity, instead of using ln$S$. The author of this doctoral thesis discourages such practice (see Section 2.3.2).

The remaining indicators included in Table 1 could be considered as descriptors of homogeneity or tree size inequality. Some are based on ranking the data and studying the Lorenz curve, such as the Gini coefficient (GC) or de Camino homogeneity (CH). The structure index based on variance (STVI) has its foundations in comparing the empirical variance (s_{DBH}^2) against theoretical distributions – uniform and maximally bimodal. A different approach would be to study forest structure by means of parameter estimation of theoretical models (Knox et al. 1989; Coomes and Allen 2007), which was not considered for this doctoral thesis, as it has been covered by previous research (Gobakken and Næsset 2004; Maltamo et al. 2007).

The list of references provided in Table 1 is not exhaustive, but a summary selection illustrating their evolution and popularity among researchers adapting them for the analysis of forest structure, along with the source of the original index. The use of the theory of information and entropy to describe forest structure is so widespread that it cannot be summarised on a table. The original index of MacArthur and MacArthur (1961) has undergone numerous modifications over the decades (Murdoch et al. 1972; Willson 1974; Aber 1979; Erdelen 1984; Ferris-Kaan et al. 1998; Berger and Puettmann 2000; McElhinny et al. 2005), such as considering vertical eveness (Neumann and Starlinger 2001). The general theory of intrinsic diversity ordering was then adapted to the study of entropy between DBH classes (Gove et al. 1994), which led to the widespread use of the Shannon index in the scientific literature (Buongiorno et al. 1994; Önal 1997a; Wikstrom and Eriksson 2000; Staudhammer and LeMay 2001; Sullivan et al. 2001; del Río et al. 2003; Harper et al. 2003; O'Hara et al. 2004; Frazer et al. 2005; Rouvinen and Kuuluvainen 2005; Lexerød and Eid 2006; Sterba and Zingg 2006; McRoberts et al. 2008; Barbeito et al. 2009; Lei et al. 2009; Pretzsch 2011; von Gadow et al. 2012; Looney and Waring 2012; Ozdemir and Donoghue 2013; Palace et al. 2015). There is also a great variety of indices which combine the various dimensions of forest structural complexity – composition, structure and function – also based on the grounds of the theory of information (Pretzsch 1995 – as cited in Pretzsch 2011 –; Lähde et al. 1999b). Using marked point process statistics (Pommerening 2002), the concept of entropy has sometimes been employed simultaneously using both horizontal structure (spatial distribution of stems) and vertical differentiation (Freemark and Merriam 1986; Zenner and Hibbs 2000).

Apart from using diversity or equitability ordering, another type of approach to describe vertical forest structure has been to employ the concept of Lorenz ordering, and its derived indicators. Using the Lorenz curve to describe homogeneity was first suggested by de Camino (1976) and Weiner and Solbrig (1984). These indicators are mainly adaptations of the Gini coefficient of tree size inequality (Weiner 1985; Knox et al. 1989; Latham et al. 1998; Rouvinen and Kuuluvainen 2005; Lexerød and Eid 2006; Bollandsås and Næsset 2007; Lei et al. 2009; Duduman 2011; Klopcic and Boncina 2011; von Gadow et al. 2012; Ozdemir and Donoghue 2013; Cordonnier and Kunstler 2014) or other measures of heterogeneity (de Camino 1976; Damgaard and Weiner 2000; Bachofen and Zingg 2001). It is also worth noting that many other authors have also simply used descriptors of the DBH distribution, such as the coefficient of variation in tree DBH (Weiner and Thomas 1986; Latham et al. 1998; Berger and Puettmann 2000; Coomes and Allen 2007; Pretzsch 2011; von Gadow et al. 2012), standard deviation or DBH differentiation indices (von Gadow 1993 – as cited in Kint et al. 2000 –; Önal 1997b; Staudhammer and LeMay 2001; Barbeito et al. 2009; Motz et al. 2010; Pretzsch 2011), and others have also focused on adding skewness (Knox et al. 1989; Sterba and Zingg 2006 – as cited in von Gadow et al. 2012 –; de Miguel et al. 2012). Lexerød and Eid (2006) and Lei et al. (2009) compared most of these diversity, equitability and homogeneity indices, finding inconsistencies with regards to their potential for discriminating between forest structural types and also to their ability to be arranged in a reliable order of structural complexity. Prior to researching the relationships between these indicators and ALS datasets, there was thus a need to further clarify which of these indices best describe forest structural diversity and tree size inequality.

1.3 Rationale: the value of forest structure indicators obtained with airborne laser scanning (ALS)

Recent advances in remote sensing provide new opportunities to monitor forest structure over large spatial scales, and increase our knowledge on ecosystem dynamics. Before the advent of remote sensing, producing a continuous inventory of forest structural complexity was considered an impossible undertaking (Latifi 2012). Thanks to ALS remote sensing, such wall-to-wall surveys are nowadays a reality, as ALS allows the identification of structural differences across broad areas of forests (Gould 2000; Smith et al. 2014). ALS can provide reliable methods to compare forest areas and evaluate canopy changes (Oliveira et al. 2007; McInerney et al. 2010). For this reason, forest managers anticipate that the possibilities of ALS for large-scale mapping will be essential to integrated ecological-economical-social management of forested environments (Burger 2009).

ALS consists of scanning the forest from a plane with a lidar sensor that measures distances by emitting laser pulses and detecting their echo. A lidar device emits about 200,000 laser pulses per second, recording the time taken for those pulses to be backscattered off terrestrial surfaces and return to the sensor. By knowing the precise position of the plane and direction of the beam, ALS systems are able to build a three-dimensional point cloud of land surfaces. Due to beam divergence, the pulse has a width of about 30-50 cm when it reaches the surface (which is called “footprint”). When the lidar footprint is targeted upon a forest canopy only a portion is backscattered off the upper crowns, while other components bounce off leaves and branches further down the canopy, and to the ground (Baltsavias 1999). Thus multiple returns are obtained from a single pulse, and ALS provides valuable information about the understory that can be used to characterise a forest’s vertical structure. ALS may therefore be used to study vertical profiles and DBH distributions (Maltamo et al. 2004), bringing numerous inventory applications to the evaluation of stand properties (Næsset 2009; Maltamo et al. 2014) or carbon stocks (Asner et al. 2012; UNFCCC 2013). Methodologies for ALS-based inventories are well established, but they require a forest compartment stratification based on a priori knowledge of the site (Naesset 2002), such as species or development class. Forest stratification – the classification of woodland area into homogeneous types, minimising within-strata variability – is amongst the most effective of methods available for scaling up remote sensing estimates (Asner et al. 2012). Concise indicators of forest structure derived from airborne laser scanning (ALS) can thus be employed for automated stratification into forest structural types (FSTs), arguably with a value in increasing the accuracy of carbon budget estimates.

ALS measurements of canopy structure can also be used to increase our knowledge on ecosystem functioning (Latifi 2012; Smith et al. 2014). They have been used as a proxy to assess wildlife distribution (Palminteri et al. 2012; Melin et al. 2014; Vihervaara et al. 2014), plant diversity (Simonson et al. 2012), tree competition (Pedersen et al. 2012), and forest growth and disturbance dynamics (Kellner and Asner 2009). ALS information on the structure of forest canopies can be used to evaluate the risk of windthrow damage (Suárez et al. 2008) the vertical continuity of fuel (Riaño et al. 2003) and the spread rate of crown fires (González-Olabarria et al. 2012). Remote sensing methods based on ALS can provide valuable information on relative abundances between DBH classes (Maltamo et al. 2007; Jaskierniak et al. 2011), or even estimate them in a species-wise fashion (Packalén and Maltamo 2008). The work carried out for this doctoral thesis was a first attempt to focus on indices of structural diversity, equitability and size variation, which could provide concise indicators summarising such large amount of information. Although there is a plethora of forest applications of ALS remote sensing (Maltamo et al. 2014), little research has compared the same methodologies in dissimilar study areas (Gatziolis 2010), so a comparative evaluation of the sustainability of different management plans remains difficult. There is therefore a need to develop indicators that can be consistently used transnationally and across ecosystem types.

1.4 Objectives

The ultimate goal of this research is to provide an objective, consistent and replicable methodology for characterising the structural complexity of forests, that can be implemented trans-nationally (e.g. at a pan-European level). Objectivity is to be attained by searching for a strong theoretical basis for the methods developed. Conciseness is to be achieved through the development of simple indicators that could allow the discrimination of a wide range of forest structural types. Replicability is to be obtained by providing a methodology based on ALS remote sensing data that could be acquired over large areas (e.g. low-density national datasets, see Section 3.4.1). Through this, our wish is to assist the development of continuous cover forestry management systems, by providing methodologies to compare different management alternatives with regards to forest complexity, evaluating the success of natural regeneration in forests, the need for specific silvicultural treatments, etc.

The author of this thesis envisions the establishment of study area-independent methodologies for forest structure mapping, towards a harmonised use of ALS systems at a pan-European level. This is an ambitious objective which can only be fully attained with a large consortium supporting a large-scale project. However, bearing this ultimate goal in mind, this doctoral thesis aspires to build the foundations to can make it possible in the future. Proceeding towards the final objective method for concise indicators obtained by ALS remote sensing, this research focused on the following sub-objectives:

1) Understand the indicators which best describe forest structural complexity among those employed in the scientific literature. (Thesis body and Study I)
2) Investigate the possibilities of using ALS state-of-the-art techniques for calculating these indicators.
    a) Analyse the relationship that ALS metrics may have with the targeted indicators, selecting those that are not only suited for forest structure characterisation, but also which can be accurately obtained with ALS remote sensing. (Studies II and III)
    b) Compare all state-of-the-art methods in ALS in order to choose the most reliable for the given indicators. (Study IV)
3) Study the capacity for the selected indicator estimates to be practical and beneficial with regard to: their ability to discriminate forest structural types, assist forest management, and monitor its effects. (Studies V and VI)

Thus, each sub-objective answers the following questions sequentially:

- What are the most suitable indicators that can be obtained from the forest data itself?
- Which of those indicators can be reliably estimated from ALS remote sensing?
- What is the best estimation method for obtaining those indicators? and
- Are the ALS predictions of the selected indicators useful for forest inventory, monitoring and management?

2 MATERIALS AND METHODS

2.1 Research areas

As the main objective is to develop a study area-independent methodology, study areas from different countries were involved in the analysis. In order to achieve generality, the study of indicators of forest structure should ideally include woodlands covering the full range of European biogeographic regions. For this reason, the analyses presented in this doctoral thesis are planned to be extended in the future. Nevertheless, such an enterprise requires more time and resources than those available for a doctoral project tackled by one person alone. Consequently, the present research has focused on conifer forests included in Mediterranean and Boreal woodlands, each undergoing very different forest management practices. The work of this doctoral thesis included study areas in Spain and Finland (details shall be scrutinised in descriptions included in the articles):

1) Mediterranean (Spain). Drought-adapted coniferous forests.
   a) **Study Area 1: Valsaín** (Studies I, II and V). Lat. 41°7′N; lon. 4°8′W; alt. 1300 – 1500 m a.s.l. Shelterwood managed Scots pine (*Pinus sylvestris* L.) high forest stands with cutting cycles of 120 years. ALS data included 800 ha acquired with a density of 1.15 pulses·m^{-2}, and field data consisted of 37 circular plots.
2) Boreal (Finland). Cold-adapted coniferous forests.
   b) **Study Area 2: Kiihtelysvaara** (Studies III, IV and VI). Lat. 62°31′N; lon. 30°10′E; alt. 130 – 150 m a.s.l. Typical boreal forest managed for production purposes: rotation periods of 70 – 90 years, including two thinning treatments. *P. sylvestris* and Norway spruce (*Picea abies* (L.) Karst.) are the most predominant species. ALS covered 800 ha acquired with an exceptionally high density of 11.9 pulses·m-2, and field data consisted of 79 plots.
   c) **Study Area 3: Koli** (Study VI). Lat. 63°03′N; lon. 29°53′E; alt. 90 – 350 m a.s.l. Managed directed at forest conservation and restoration. Although *P. sylvestris* and *P. abies* are also the dominant tree species, various admixtures of deciduous species are present as well. ALS data included 2200 ha flown with a density of 3.9 pulses·m-2, and field data consisted of a total of 47 plots.

2.2 Forest Structural types (FSTs)

Forest plots were classified into forest structural types, with the intention of shedding some light to the indicators analysed. This classification was done visually in the field, and also by interpretation of the empirical DBH frequency and basal area weighted distributions of each plot (white and grey bars, respectively, of histograms included in Fig. 3, see results). Study I includes a detailed description of these FSTs, and Study V describes the silvicultural treatments leading to each in the type of shelterwood management carried out in Valsaín. These FSTs can be classified as:

- *Single-cohort (Even-sized)*. Frequently characterised by the shape of a normal distribution in both their DBH frequency and basal area-weighted histograms. This research also differentiated even-sized areas comprising young *poles* from *mature* ones containing larger trees (see Studies I and V: Figs. 1a-b). Within this group can also be included mature stands where disturbance has opened a gap in the canopy and seedlings began sprouting: early stages of natural understorey *reinitiation* (Study V: Fig. 1c).

- *Uniform (Irregular)*. The reference for this FST would be a theoretical uniform DBH frequency distribution (Study I: Fig. 1). It could also be called multimodal. The main idea is that stem frequencies are more or less uniformly distributed over a multiplicity of DBH classes, what means that the proportions of basal area increase towards the bigger DBH classes.
- *Reverse J*. This FST is represented by an ideally balanced structure with a constant *q*-ratio[3], the archetype of continuous cover forestry (Schütz et al. 2012). This research also differentiated whether a balanced reverse J could be approximated to a negative exponential function, or whether large trees coexisted with saplings and therefore the shape was that of a *peaked reverse J*, more similar to an earlier stage prior to becoming a bimodal FST (Studies I and V: Fig. 1d-e).
- *Two-cohort (Bimodal).* Forest areas with a sub-dominant cohort established in the understorey (Studies I and V: Fig. 1f). They are difficult to generalise, as different functions may apply to each cohort (e.g., Coomes et al. 2003; Jaskierniak et al. 2011)

2.3 Deductive reasoning: theory of information and intrinsic ordering

This stage aimed to answer the first objective of this doctoral thesis (Study I): what are the best indicators to describe horizontal differentiation? Many authors have reported unsatisfactory results when using diversity indices (von Gadow 1993 – as cited in Kint et al. 2000 – Harper et al. 2003; Rouvinen and Kuuluvainen 2005; O'Hara et al. 2007; Barbeito et al. 2009), giving a general feeling that diversity indices are inconsistent with the properties that they are meant to describe. Others found forest structure to be more related to measures of DBH dispersion or equitability than to diversity indices (Knox et al. 1989; Staudhammer and LeMay 2001; Lexerød and Eid 2006; McRoberts et al. 2008). Heuristic methods based on inductive statistical indications have, however, been used to reach these conclusions. Correlations between diverse indices, or statistical differences found among forest structural types, for instance, have been used before. Little effort has been invested in examining the implications of adapting those indices to the study of tree size classes, whether it complies with the definition of diversity and its mathematical interpretation, or assuring that the basic assumption underlying the calculation of these indices are not violated. This assumption is that two populations can only be compared by means of a diversity index whenever they keep consistency in their intrinsic diversity ordering[4] (Patil and Taillie 1982; Lambshead et al. 1983). Similarly, two populations can only be compared by means of an equitability (evenness) index if they have consistent intrinsic equitability ordering[4] (Studeny et al. 2011).

Study I questioned the convenience of comparing empirical DBH distributions – unweighted and basal area-weighted – using the indices detailed in Table 1. The deductive approach used was based on intrinsic ordering methods: intrinsic diversity, intrinsic equitability, and Lorenz ordering. The mathematical theory of information was revised, relating many of the indicators in Table 1 through generalised entropy (Legendre and

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[3] The ratio between the number of stems in a DBH class and the consecutive one, i.e. a constant sequence decreasing the number of stems while increasing DBH.

[4] The accumulated dominance among their DBH classes is consistently higher or lower (see Sections 2.3.1 and 2.3.2, and references provided: Patil and Taillie (1982), Lambshead et al. (1983), etc.). In other words, ranked accumulated distribution of their abundance vectors (for diversity) or relative abundance vectors (for equitability) do not intersect.

Legendre 2012) and generalised equitability numbers (Hill 1973). This yielded diversity and equitability profiles, showing many of these indices at once. In addition to intrinsic ordering, diversity and equitability profiles were also computed, illustrating the inconsistencies found for some of those indices, and their inability to arrange dissimilar forest structural types in a logical order.

2.3.1 Intrinsic diversity ordering

With the intention of dealing with the problem of inconsistent ranking between diversity indices, and thus assisting the choice of indicators, a mathematical theory of index sensitivity was developed by Patil and Taillie (1977). The definition of diversity implies that an initial situation in the structure of a forest plot can develop into an intrinsically more diverse state by a finite sequence of these events: (a) introducing new DBH classes, (b) transferring abundances between two DBH classes to make them more identical, or (c) that it should remain equally diverse when permuting the components of the abundance vector. When comparing two plots, this can be proven true if their accumulated dominance at each size class is always lower: their intrinsic diversity ordering is consistent. Solomon (1979) proposed the use of majorization $I_k(k, M_k)$ to test intrinsic diversity ordering, although there is a wide range of other methods available (Liu et al. 2007).

Essentially, diversity indices measure entropy (Legendre and Legendre 2012). When diversity indices are applied to studying horizontal differentiation, they measure the entropy of either the DBH distribution function (unweighted) or the basal area-weighted distribution function. Relative abundances $\mathbf{p} = \{p_i\}$ are considered for DBH classes $i = 1, \dots, S$. When adapting the diversity indices to the study of DBH distributions, **p** can be defined as either the relative proportions of basal area ($p_i = g_i/G$) at each DBH class (see Table 1) or the relative frequency of number of stems ($p_i = n_i/N$) at each DBH class[5]. In order to test for intrinsic diversity ordering, the abundance vector **p** has to be arranged in order, obtaining a ranked abundance vector $\mathbf{p}^{\#} = \{p_k^{\#}\}$, where $k = 1, \dots, S$ is the rank of each DBH class. A cumulative ranked abundance curve can then be computed, yielding an intrinsic diversity profile $I_k(k, M_k)$ where:

$$M_k = \sum_{j=1}^{k} p_j^{\#} \; (k = 1, \dots, S) \qquad (1)$$

When the intrinsic diversity profile of tree population lies completely below another population’s profile, then it can be said that it has more diversity of DBH classes (Patil and Taillie 1982), as it complies with the above-mentioned definition of diversity – i.e. one could develop to another through either (a), (b) or (c). If their profiles intersect, however, there would be no intrinsic ranking between them, and they could not be compared by means of a diversity index. For this reason, diversity indices may be inconsistent if no intrinsic ordering is assured.

2.3.2 Intrinsic equitability ordering and Lorenz ordering

As explained (see Section 1.2), a measurement of structural diversity comprises both the richness of DBH classes and the equitability of relative abundances between them (Magurran 2004). There may be interest in studying the inequality between DBH classes independently

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[5] This would be the unweighted version of those same indices, as suggested in Table 1

to their quantity. This can be done if richness is also rescaled into cumulative proportions (Studeny et al. 2011), being $\mathbf{x} = \{x_k\}$, where $x_k = k/S$. This yields a Lorenz curve $P_k(x_k, M_k)$. In fact, Lorenz equitability ordering is equivalent to intrinsic diversity ordering methods for cases of equal richness (Lambshead et al. 1983). Conversely, the intrinsic diversity ordering scale is normalised by richness, and ranks are arranged by cumulative proportions of total richness at plot level. Thus, P_k becomes an intrinsic equitability ordering method. Intrinsic equitability ordering can then be used as a method for testing the suitability of indices describing equitability (eveness) between relative abundances. This is the case for any categorical variable, such as species or DBH classes. However, DBH is, in fact, a continuous variable, and many authors have discussed the inconvenience of having to decide on a bin size for apportioning DBH classes (von Gadow 1993; Staudhammer and LeMay 2001; Barbeito et al. 2009).

For computing Lorenz curves, the most common procedure is to accumulate a continuous variable. Since this is the case for the basal area $\boldsymbol{g} = \{g_t\}$ of individual trees $t = 1, \dots, N$, separating into discrete DBH classes is unnecessary, as trees can themselves be ranked according to their DBH. Instead of DBH class ranks k, we obtain tree DBH ranks $r = 1, \dots, N$, and the ranked vector of relative abundance $\boldsymbol{g}^{\#} = \{g_r^{\#}\}$, which can be accumulated as:

$$M_r = \sum_{j=1}^{r} p_j^{\#} \ (r = 1, \dots, n), \text{where } p_j^{\#} = g_j^{\#}/G \qquad (2)$$

The Lorenz curve of tree DBH inequality $L_r(x_r, M_r)$ can be plotted to identify the relative increase in basal area accounted by each tree, reflecting the relative dominance of each tree compared to those surrounding it. Since $x_r = r/N$ (as compared to $x_k = k/S$ for P_k), we shall also express x_r as:

$$x_r = \sum_{j=1}^{r} p_j^{\#} \ (r = 1, \dots, N), \text{where } p_j^{\#} = n_j^{\#}/N = 1/N \qquad (3)$$

Equations 2 and 3 then illustrate that L_r is a normalisation of the accumulated abundance in terms of basal area expressed by the accumulated abundance in terms of number of trees. Therefore, in the Lorenz curve of DBH inequality the relative dominance is simultaneously studied for both the unweighted DBH distribution (Eq. 3) and the basal area-weighted distribution (Eq. 4).

Intrinsic ordering was thus the method employed to address the first objective of this doctoral thesis (see Section 1.4): understanding the indicators which best describe forest structural diversity, and selecting the most suitable indicator from those employed in the scientific literature (Table 1). Intrinsic diversity $I_k(k, M_k)$, intrinsic equitability $L_k(x_k, M_k)$, and Lorenz ordering $L_r(x_r, M_r)$ was tested for several forest plots. Forest structural types were identified at those plots, with the intention to shed light on the meaning that the indicators suggested in Table 1 may have in terms of describing the structural properties of forests. Although this methodology was carried out for all the field plots available in Valsaín, only a few plots– each representative of a given forest structural type – were selected for use in writing a scientific article corresponding to the results in Study I (this thesis body details the results in full, see Section 3.1.2). This was done for the sake of clarity, as only one case violating the assumption suffices to render a given index inadequate for comparing the contrasted populations. This part of the analysis therefore lacked any statistical inference (Barabesi and Fattorini 1998), and the arguments for choosing from the indices in Table 1 were simply based on deductive reasoning related to their mathematical properties. The final outcome of this stage was the set of indicators finally selected, as detailed below, as target response $\boldsymbol{Y} = \{y_i\}$.

2.4 Inductive exploratory multivariate analysis: relationships between ALS metrics and forest structure indicators.

The next stage involves the second objective of this doctoral thesis: to investigate the possibilities of using ALS for estimating these chosen indicators. Inductive exploratory analysis was used to study the relationships between ALS metrics and targeted indicators, and the capacity of ALS remote sensing to predict these was tested. Once the Lorenz curve was screened as the most reliable method for characterising horizontal differentiation in tree populations, two approaches to exploratory multivariate analysis were carried out. The first approach involved the use of the selected indicators and their components as a response (Study II). The second involved analysing the relationships of ALS metrics along the entire Lorenz curve, revealing the capacity of these predictors to describe the relationships of relative dominance among trees in the forest (Study III).

Procedures for computing the ALS metrics which were used as predictors were those of widespread use in area-based approaches for ALS remote sensing (Maltamo et al. 2014). The ALS returns were processed, filtered and classified using Terrascan software (Terrasolid, Finland). Returns from the ground were filtered following Axelsson (2000), with the remainder being classified as vegetation. Ground points were interpolated into digital terrain models which were used to subtract the ground level from individual ALS returns and obtain their heights above ground. The ALS data corresponding to each plot was clipped, and metrics from their heights were computed with FUSION software (version 3.1, McGaughey 2012). These ALS metrics were moment, order and quantile statistics (Magnussen and Boudewyn 1998; Næsset 2002), L-moments and their ratios (Hosking 1990), and canopy cover metrics (McGaughey 2012; see summary of ALS metrics in appendix). The outcome was an array of predictors $\boldsymbol{X} = \{x_j\}$ for $j = 1, \dots, p$ field plots. They were computed at plot-level and used for the exploratory multivariate analysis of their relationships with the target indicators $\boldsymbol{Y}$, which employed various methods: correlation, multi-model inference, partial least squares (Study II), and canonical correlation analysis (Study III). Some of these procedures were also used as grounds for predictor selection or feature space transformation in the predictive application pursued later, as explained below (see Section 2.4).

Although the scale of each predictor has no effect on their predictive ability, methods devoted to inductive multivariate exploration of the relative importance of each predictor on the explained variability over the response usually require a prior standardisation of variables. Standardising the response also allows comparing which indicators are more closely related to the ALS metrics. For this reason, z-standardisation was carried out for all variables (Frank and Friedman 1993). Original cases were transformed into z-scores comparable to a standard normal distribution N(0,1), by subtracting their sample mean and dividing by their sample standard deviation:

$$x_i \leftarrow (x_i - \bar{x})/s_{\mathrm{x}} \tag{4}$$

2.4.1 Multi-model inference (MMI)

An information-theoretic approach for multi-model inference (MMI; Sakamoto et al. 1986; Burnham and Anderson 2002) was followed for evaluating the relative importance of each predictor x_j in explaining variance in the response $\boldsymbol{Y}$. For each response variable, a list of candidates was generated with all plausible combinations of $\boldsymbol{X}$. The parsimony of the models was thereafter compared by means of AIC-corrected for finite samples ($AICc$) (Sakamoto et al. 1986; Sugiura 1978). For the p ALS metrics selected in each case, model estimates $\boldsymbol{\beta} = \{\hat{\beta}_0, \hat{\beta}_1, \dots, \hat{\beta}_p\}$ were least squares-adjusted and tested for significance in their linear form (transformations were also included within $\boldsymbol{X}$ and $\boldsymbol{Y}$, when applicable; see Section 2.5.1), from the training dataset:

$$y_i = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j x_{ij} + \varepsilon_i \text{, where } i = 1, \dots, m \text{ and } \varepsilon_i \sim \mathrm{N}(0, \sigma_i) \tag{5}$$

The MMI approach takes all alternative models into account simultaneously. The relative increase in $AICc$ for all k candidate models with respect to the best subset was evaluated by a delta parameter Δ_k, which substracted the minimum value of $AICc$ obtained by the best combination of predictors (see best subset selection in Section 2.4.1). Model averaging was performed, selecting, among the k candidate models, those under a $\Delta_k < 2$ threshold (Burnham and Anderson 2002: 170). A list $\hat{\boldsymbol{m}} = \{\hat{m}_k\}$ of l models compiling with this criterion was used to calculate the final model estimates as weighted averages (Burnham and Anderson 2002: 283), the weights being the relative likelihood of each model:

$$\hat{\hat{m}} = \sum_{k=1}^{l} \frac{\mathrm{e}^{-\Delta_k/2}}{\sum_{j=1}^{l} \mathrm{e}^{-\Delta_j/2}} \{\hat{m}_i\} \tag{6}$$

The relative variable importance in the final averaged model was considered as the sum of all weights of those models where the given variable was involved (Burnham and Anderson 2002:168). Exploratory multivariate analysis was carried out by means of this relative variable importance, which provided an idea of which ALS metrics explained more variance in the target indicators. Although MMI was at first considered for predictive purposes, the results obtained discouraged the use of MMI for this task, as model averaging yielded a final over-parameterised model containing too many predictors, possibly leading to over-fitting (see Study II).

2.4.2 Partial least squares (PLS)

In partial least squares (PLS), linear combinations of the response and predictors are iteratively multiplied by the covariance with the opposite space, until reaching convergence:

$$\mathbf{P} = (1/n)\mathbf{X}^{\mathrm{T}}(\mathbf{YQ}) \tag{7.1}$$
$$\mathbf{Q} = (1/n)\mathbf{Y}^{\mathrm{T}}(\mathbf{XP}) \tag{7.2}$$

Where n denotes the sample size, while $\mathbf{Q}$ and $\mathbf{P}$ are the coefficients for those linear combinations of response and predictors, respectively. After obtaining one component, the variability explained by the scores is extracted from the original variables. Let **T** be the x-scores and **Q'** are the y-loadings (Valbuena et al. 2012):

$$\mathbf{X}_{res} = \mathbf{X} - \mathbf{TP}^{\mathrm{T}} \tag{8.1}$$
$$\mathbf{Y}_{res} = \mathbf{Y} - \mathbf{TQ}'^{\mathrm{T}} \tag{8.2}$$

The next PLS component is computed from the residuals of the previous one ($\mathbf{X}_{res}$ and $\mathbf{Y}_{res}$). The NIPALS algorithm (Wold 1975) forces them to be orthogonal scores. As a result, the original multidimensionality is compressed into a few significant PLS components which account for successively lower proportions of the explained variance $\{PLS_1, PLS_2 \dots\}$. The correlation plot between these components was drawn to identify the relative importance of each predictor, and also their relationships with the response variables (Mevik and Wehrens 2007). As the explained variance between response and predictors is partitioned, PLS is well suited for analysing complex relationships involving opposed effects, and it was therefore selected for the analysis of Lorenz curve's asymmetry (as the indicators involved intrinsically had an inverse relationship to one another, see Study II). The use of PLS for predictive purposes was also discouraged by over-fitting effects observed in previous research (Valbuena et al. 2012), and therefore PLS was also employed only for exploratory multivariate analysis.

2.4.3 Canonical correlation analysis (CCA)

The outcome of a canonical correlation analysis (CCA) is similar to that of a PLS, in the sense of compressing the original multidimensionality into few components emphasising the significant relationships between $\boldsymbol{X}$ and $\boldsymbol{Y}$ (Nash et al. 2005). In the case of CCA, the procedure maximises $\text{cov}(\boldsymbol{X}, \boldsymbol{Y})$, also computing linear combinations of the response ($\mathbf{U}$) and predictors ($\mathbf{V}$):

$$\mathbf{U} = \boldsymbol{\alpha}\mathbf{Y} \tag{9.1}$$
$$\mathbf{V} = \boldsymbol{\gamma}\mathbf{X} \tag{9.2}$$

where $\boldsymbol{\alpha}$ and $\boldsymbol{\gamma}$ are the canonical coefficients of $\boldsymbol{X}$ and $\boldsymbol{Y}$, respectively (Gittins 1985). There are as many canonical coefficients as plausible combinations of canonical $(\boldsymbol{V}, \boldsymbol{U})$ bivariates which, arranged in order of descending correlation, yield a set of CCA components $\{CCA_1, CCA_2 \ldots\}$ that compresses the original dataset into those statistically significant with regards to maximising the explained variance. CCA analysis was also employed for exploratory multivariate analysis, selecting it for the analysis of the entire Lorenz curve due to its ability to deal with a multivariate response (Study III). Contrary to the other methods carried out in the exploratory stage, CCA was also used for predictive purposes, as it has become common to compute CCA to maximise the covariability and transform the feature space in nearest neighbour imputation, a procedure termed the "most similar neighbour" estimation (MSN; Moeur and Stage 1995; see section 2.4).

2.5 Predictive modelling: wall-to-wall ALS estimations of target indicators.

The last step in fulfilling the second objective of this doctoral thesis was to compare a wide range of state-of-the-art methods in ALS remote sensing in order to choose the most reliable for estimating the given indicators (Study IV). ALS prediction methods roughly divide in two main types of approaches (Maltamo et al. 2014): those based on individual tree detection (ITD), and the so-called area-based approach (ABA) (Fig.2). The former will be only briefly introduced, as the author of this doctoral thesis did not personally engage in their development, instead focusing on the multiple options for ABA. The reason for choosing ABA was that segmentation procedures for the ITD method usually require higher scan densities for reliably identifying individual trees. ABA was therefore foreseen as a more realistic approach for practical implementation for low-density country-wide datasets, and thereby the pan-European scale, in the future.

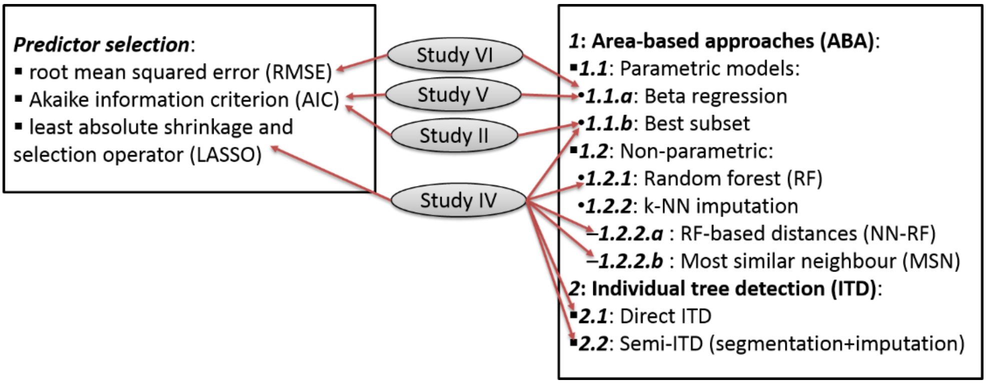

Figure 2. Summary of combinations of indicator estimation methods (left) and predictor selection criteria (right) employed in each of the studies which involved indicator predictions (middle).

The set of predictors $\boldsymbol{X} = \{x_j\}$ used for training in predictive modelling was the same as explained for the exploratory analysis (see Section 2.3). As is commonplace in ABA, the models were afterwards implemented with the same metrics computed over a grid covering the entire study areas wall-to-wall (Næsset 2002). $\boldsymbol{Y}$ has essentially been the target forest structure indicators, which underwent slight changes in the course of the work of this doctoral thesis. Different parametric models and variable selection procedures for their direct estimation were tested across articles (Studies II and IV-VI). Study IV also tested a number of non-parametric methods. Study IV also tested the convenience of changing the estimated response $\boldsymbol{Y}$ into complete DBH distributions or entire Lorenz curves, as they provide more detailed information from which the forest structure indicators can be derived afterwards (Study IV: Fig.1). Non-parametric methods permitted this, as they can tackle the estimation of larger number of response variables simultaneously. For this reason, it was decided to also test the possibility of applying estimation procedures not aimed directly at the target indicators, but at the DBH distribution or the Lorenz curve itself. The response set was thus also considered to be discrete quantiles along the Lorenz curve, and thus $\boldsymbol{Y} = \{M(x_r)\}$ for $x_r = \{.05, \dots, .95\}$ (eqs. 2-3; Studies III-IV; strategy B sensu Study IV). In the case of DBH frequency distribution estimation, the response became $\boldsymbol{Y} = \{p_i\}$ for all the DBH classes $i = 1, \dots, S$ (strategy C sensu Study IV). We considered only the estimation of unweighted distributions $p_i = n_i/N$, since Gobakken and Næsset (2004) and Maltamo et al. (2007) showed that ALS estimation obtains similar results for weighted and unweighted distributions.

Figure 2 shows how many combinations of approaches were tested and compared. The reason for this is that the author of this thesis sought to improve the previous approaches whenever facing a new study area and a new estimation procedure. The convenience of either estimation method can depend on each response variable, and perhaps its empirical distribution and relationship with the ALS metrics (see appendix). The state-of-the-art is also especially unclear with regards to the most convenient variable selection method, whose result seemly affects the final accuracies critically. This was also the reason for carrying out a detailed multivariate exploratory analysis (Section 2.4), which is suggested as a method superior to any automated statistical technique.

Table 2. List of models and corresponding variable transformations.

	Transformations	Model	Linearized
Linear	-	. $y_i = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j x_{ij}$	-
Logarithmic	$\ln(x_j)$	$y_i = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j \ln(x_j)$	-
Exponential	$\ln(y_j)$	$y_i = \exp(\hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j x_{ij})$	$\ln(y_j) = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j x_{ij}$
Multiplicative	$\ln(x_j)$; $\ln(y_j)$	. $y_i = \hat{\beta}_0 \cdot \prod_{j=1}^{p} \hat{\beta}_j x_{ij}$	$\ln(y_j) = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j \ln(x_j)$
Sigmoidal	$\ln(1/x_j)$	$y_i = \hat{\beta}_0 + \sum_{j=1}^{p} \hat{\beta}_j \ln(1/x_j)$	-

2.5.1 Linearized models and variable transformations

Many variable transformations were tested, in order to consider the possibility of non-linear relationships existing between the predictors and the response. All models in Table 2 were considered, and thus the relationships between the forest structure indicators and the ALS metrics were analysed through their ensuing variable transformations.

2.5.2 Best subset selection via Akaike Information Criterion (AIC)

This estimation method followed the procedures described for MMI (Section 2.3.1). As model averaging was considered a disadvantageous choice for predictive purposes, easily leading to over-fitting, the outputting table raking models by $AICc$ was employed to select the most parsimonious model (Sakamoto et al. 1986). From all the k candidate models yielded from Eq. 5, the criterion of min $AICc_k$ was used to select the best subset of predictor variables (Hudak et al. 2006). This was the method employed for linear model estimations involved in this doctoral thesis (Studies II and IV).

2.5.3 Beta regression.

Once it was realised that the value of the chosen target indicators was confined to a [0,1] range (note indicator modification in Study V), beta regression was considered an advantageous modelling technique. Beta regression is a special type of generalised linear model (Ferrari and Cribari-Neto 2004), which consists of estimating the mean μ and variance ϕ parameters of the theoretical beta distribution which best fits the response (univariate in this case, $\boldsymbol{Y} = y_i$) by maximum likelihood:

$$y \sim \text{Beta}(\mu, \phi), \text{ where } \mu \in [0,1] \tag{10}$$

Where the μ parameter is estimated through its relationship to the predictors $\boldsymbol{X}$, which are related to it by a logit link function (which becomes the response in Eq. 5: see details in Study V). Consequently, the density function of the response estimate can be expressed as a function of the model coefficients.

$$y \sim \mathrm{Beta}\left(\frac{\exp(\boldsymbol{X}^{\mathrm{T}}\boldsymbol{\beta})}{1+\exp(\boldsymbol{X}^{\mathrm{T}}\boldsymbol{\beta})}, \phi\right) \tag{11}$$

As a result, the predictive range of y is kept within its theoretical limits, as the logit function is asymptotic in the range [0,1]. $\boldsymbol{X}$ was defined in each case by a previous predictor selection procedure (Fig. 2). The variable sets employed for Study V were selected using the information derived from the prior exploratory multivariate analysis (Study II): no systematic procedure was carried out as it was felt preferable to make a logical selection on the most beneficial predictors. On the other hand, Study VI based its variable selection on a procedure of exhaustive comparison of all plausible model combinations (as in Section 2.3.1). In this case the criterion for choosing the best subset model was not $AICc$, but the cross-validated root mean squared error (RMSE) was minimised instead (see Section 2.5.1).

2.5.4 Least absolute shrinkage and selection operator (LASSO)

For the non-parametric methods (Sections 2.4.5 and 2.4.6) a prior variable selection was carried out using the least absolute shrinkage and selection operator (LASSO) method for variable selection (Tibshirani 1996). LASSO is a predictor shrinkage method, which is a special case of a penalized least squares method called ‘elastic net’. It minimises the L1-norm of the coefficients, the Manhattan distance. This procedure leads to many coefficients becoming zero, and therefore LASSO can be used as a variable selection method. The optimisation algorithm, the least angle regression (LARS) (Efron et al. 2003), was used to compute the entire path of LASSO solutions by stage-wise additive fitting (see details in Study III).

2.5.5 Random Forest (RF)

Random Forest (RF)[6] belongs to a group of statistical methods based on the assemblage of a collection of models and combined to leverage their collective strengths (Brosofske et al. 2014). Specifically, RF involves bootstrapping (random sampling with replacement) the training dataset and computing classification and regression trees (Hastie et al. 2009). It is therefore a method based on recursive partitioning of random permutations, were iterations are fitted by regression, so that the variable and threshold for dichotomous split at each node are selected under the criterion of minimum residual sum of squares. New additive terms are recursively included according to an exponential loss function (Hastie et al. 2009). The outcome was 500 regression trees from which their mode was selected for the final RF imputation.

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[6] In a doctoral thesis dealing with forest structure indicators, a concept to perhaps clarify for the unspecialised reader, so as to avoid confusion, is that RF refers to a statistical method and not patterns of tree spatial positions; i.e. “random” does not refer to trees having a horizontal structure following a Poisson distribution, in this context.

2.5.6 *Nearest neighbour (NN) methods.*

The work of this doctoral thesis involved an assortment of procedures involving nearest neighbour methods, in particular, the most similar neighbour (MSN). NN performs an estimation based on computing statistical distance metrics to reference sample plots in the feature space $\boldsymbol{X}$. The distance metric can be calculated following a variety of methods: Euclidean distances[7] (usually knows as k-NN; McInerney et al. 2010) the random forest algorithm (NN-RF; Hudak et al. 2008) and the canonical correlation analysis (MSN; Packalén and Maltamo 2008). The latter two, NN-RF and MSN, transform the feature space according to its relationship to the response. The imputation in NN-RF is based on the RF proximity matrix. In MSN, on the other hand, the feature space is substituted by the significant canonical correlation components (Moeur and Stage 1995). The use of canonical correlation analysis to calculate the distance metric for imputation makes the MSN method well-suited to situations requiring a multivariate response (Packalén et al. 2012). These methods were also repeated for various types of response. They were used to estimate the targeted indicators directly, but also discrete quantiles along the Lorenz curve $\boldsymbol{Y} = \{M(x_r)\}$ (see Section 2.4). MSN was also employed to estimate entire tree lists including ABA, where the imputed response is the DBH frequency distribution ($\boldsymbol{Y} = \{p_i\}$) (Packalén and Maltamo, 2008). It was also combined with ITD methods (Vauhkonen et al. 2014), into the so-called semi-ITD approach (Breidenbach et al. 2010).

2.5.7 *Individual tree detection (ITD) methods*

Individual tree detection (ITD) methods are based on identifying individual trees from a canopy height model (CHM)[8] and segmenting it into individual crowns. Field data requires accurate individual tree positions, which were available for Kiihtelysvaara, so that they can be linked to individual crown segments to train the estimation procedure. The linkage between the resulting ITD segments and the field information was carried out using MSN imputation (although, in this case data is treated per-tree, and not per-plot as in ABA). Study IV also involved another variety called semi-ITD, which links to a segment all trees measured within, as they are all considered to be represented by that segment, and not just the dominant tree (Breidenbach et al. 2010).

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[7] Although NN imputation using Euclidean distances was also computed in this research work, results for NN were excluded from the publication of Study IV, as they were regarded as adding little additional information compared to the other methods presented.

[8] A canopy height model (CHM) is a raster file obtained after processing the (vectorial) ALS data into an image-like product showing the heights above ground of canopy elements. It is commonly obtained after subtracting the height of the digital terrain model from a digital surface model enclosing the ALS returns backscattered from the vegetation. These digital models are interpolations of returns previously classified as ground or vegetation (Axelsson 2000).

2.6 Accuracy assessment.

2.6.1 *Quantitative: forest structure indicator prediction*

An accuracy assessment was performed by leave-one-out cross-validation, so that after removing one case cv at a time from the sample dataset, the entire modelling procedure – including variable selection and model training – was repeated at each iteration (Packalén et al. 2012). In order to evaluate the performance of the final model prediction, the predictor variables from the removed case (x_{cv}) were thereafter applied in each adjusted model to estimate the response. The discrepancy between the observed (y_i) and predicted ($\hat{y}^{cv}$) values could therefore be evaluated by their mean difference (bias), and also the predicted sum of squares ($PRESS$) $\sum_{i,cv=1}^{m}(y_i - \hat{y}^{cv})^2$. The root mean squared error (RMSE) was therefore obtained in the cross-validation, and relative accuracy figures were also obtained by dividing the observed mean values.

$$\text{bias} = \sum_{i,cv=1}^{n}(y_i - \hat{y}^{cv})/n \qquad (12.1)$$

$$\text{RMSE} = \sqrt{PRESS/n} \qquad (12.2)$$

Cross-validation was also used to assess the risk of over-fitting by means of the q-value (Weisberg 1985). The q-value evaluates the ratio between this cross-validated accuracy and the internal accuracy of the model, i.e. the sum of squares of residuals ($SS = \sum_{i=1}^{m}(y_i - \hat{y}_i)^2$) obtained without cross-validation:

$$\text{q-value} = \sqrt{PRESS}/\sqrt{SS} \qquad (13)$$

2.6.2 *Qualitative: forest structural types classification*

As the third objective of this doctoral thesis also included a study of the ability of the estimated indicators to discriminate between forest structural types, Study V also involved an assessment of the accuracy of the final FST classification. A cross-validated contingency matrix was also elaborated in a leave-one-out fashion. Bias was assessed as the discrepancy between the producer and user's accuracies for each forest structural types. The degree of misclassification was evaluated through the final overall accuracy and Cohen's (1960) kappa coefficient (κ).

2.7 Statistical inference.

2.7.1 Model significance and uncertainty of predictions

The significance of correlations was assessed by approximating a Student's t distribution as indicated in Study II: Eq. 8. Ordinary procedures were followed for assessing the significance of linear models: z-tests for coefficients and Fisher's test for the overall model (Study II: Table 4; Study IV: Table A2). As beta regression models were adjusted by maximum likelihood, their significance was assessed according to the likelihood ratio between the resulting adjusted density distribution (eq. 11) and the goodness-of-fit without predictors (eq. 10), testing significance with a χ^2 distribution (Study V: Table 4; Study VI: Table 1). The distribution of estimation uncertainty was observed over the final prediction maps, to assure its independence from the predictions themselves. This was done by computing standard errors of estimates wall-to-wall (Study II: Appendix B), so that computing confidence intervals from a Student's t distribution would be a straightforward procedure. While the significance of PLS components was determined by cross-validation (Study II), significance was determined for CCA components by a Fisher's test (Study III). Otherwise, non-parametric methods employed for estimation in Study IV involved no significance test, and their reliability was simply tested through the accuracy assessment procedures explained in Section 2.5.1.

2.7.2 Hypothesis testing

Study VI involved a comparison of forest areas (subpopulations) with differing history in their management regimes, in order to support the third objective of this doctoral thesis. Hypothesis testing between different subpopulations was based on statistical measures of moments of the final indicator predictions. Subpopulation means were pair-wise compared in separate one-to-one contrasts. Non-parametrical contrasts for equality of means were conducted using a Mann–Whitney U test. Multiple contrasts for means were carried out with Tukey's honest significant differences test. Within-subpopulation variances were compared with Levene's tests of equality of variances. Kolmogorov-Smirnov tests was used to compare the shapes of subpopulation distributions, via their cumulative distribution functions.

3 RESULTS AND DISCUSSION

3.1 The non-concept of structural diversity[9]

3.1.1 The challenge: diversity indices yield inconsistent results

The results obtained when calculating the indices in Table 1 were unexpectedly dissatisfying. Many of the indicators were apparently unable to discriminate even-sized from uneven-sized forests, including in some of the most obvious cases. Once the forest plots were classified into FSTs, a number of inconsistencies in the computed indicators became apparent. Figure 3 shows examples of values of all indicators from Table 1, so that their relationship to each DBH frequency and basal area-weighted distributions can be assessed numerically. Histograms in Fig. 3 represent the unweighted (white bars) and basal area weighted (grey bars) frequency distributions of plots belonging to different FSTs, whereas the vertical red line represents the position of their quadratic mean diameter (QMD). Visual interpretation can also be carried out by noting how all the values compare in Fig. 4. Scatterplots in this figure show individual field plots arranged by weighted DBH variance (the formula shown in Table 1 for the structure index based on variance) following the rationale used by Staudhammer and LeMay (2001). Some of the indicators showed quite erratic behaviour, apparently increasing or decreasing in a rather random manner. A close examination of the results obtained from the Shannon diversity index (H'), perhaps the most popular of all indices (Section 1.2.1), it can be appreciated that there are a number of inconsistencies. Note, for instance, how seedling sprouting leads to an increase in H' in early stages of re-initiation of a new cohort in the understory, but this same index decreases as the understory develops, into a peaked reverse J or as bimodal. When diversity indices are weighted by basal area, as many authors advise (Solomon and Gove 1999; Lexerød and Eid 2006), relationships to either the weighted DBH variance or FSTs themselves are even more difficult to grasp (Fig. 4).

Perhaps the most useful indicators based on the theory of information were those measuring equitability (evenness indices), when unweighted. They marked quite clear differences between bimodal and reverse J distributions and even-sized areas, but failed to discriminate irregular forest areas. Indicators based on richness (i.e. number of DBH classes) were more useful as well, in this case more so if weighted by basal area (unweighted versions substitute G by N at formulae in Table 1). Study I describes how, using parametrized entropy, it is possible to relate all these indices to generalised diversity and equitability numbers, portraying the concept of diversity as a joint representation of both richness and equitability (Study I: eqs. 8-9). These results support the idea that, in describing forest structure, these two concepts of richness and equitability should be expressed separately rather than together into a single diversity index (Hulbert 1971). Authors making use of the concept of equitability may have therefore obtained more successful results (Lexerød and Eid 2006), some having obtained a similar effect by simply dividing a diversity index by its maximum possible value[10] (e.g. Buongiorno et al. 1994).

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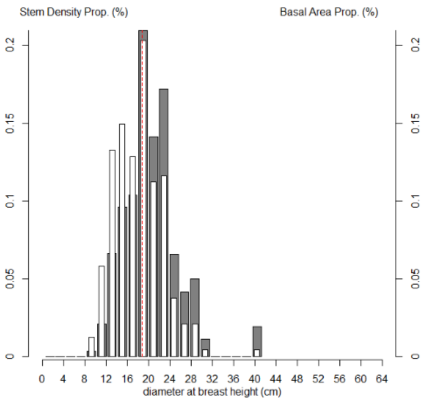
[9] Paraphrasing Hulbert (1971)

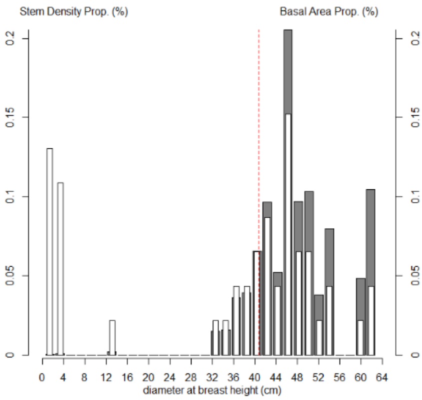
[10] This works especially well with Shannon, as it is heavily influenced by richness (observe the continuum rarity-richness-dominance in diversity numbers profiles, explained by Eq. 5 in Study I), and therefore yields a similar effect as dividing by the number of DBH classes.

(a) even-sized / single-cohort



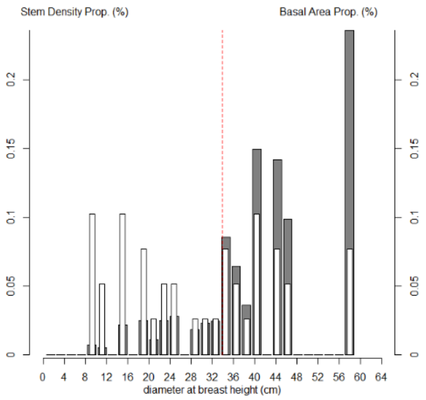
Unweighted $p_i = n_i/N$	Weighted $p_i = g_i/G$
$D_{Mg} = 2.19$	$D_{Mg} = 3.02$
$D_{Mn} = 0.387$	$D_{Mn} = 1.78$
$D_{BP} = 0.797$	$D_{BP} = 0.790$
$D_{Si} = 0.870$	$D_{Si} = 0.873$
$E_{1/D} = 0.593$	$E_{1/D} = 0.604$
$H' = 2.18$	$H' = 2.23$
$J' = 1.98$	$J' = 2.05$
$D_{MI} = 0.684$	$D_{MI} = 0.745$
$E_{MI} = 0.885$	$E_{MI} = 0.890$
	$GC = 0.272$
	$CH = 3.71$
	$STVI = 0.154$

(b) disturbance / re-initiation / regenerating



$D_{Mg} = 4.18$	$D_{Mg} = 4.13$
$D_{Mn} = 2.51$	$D_{Mn} = 2.46$
$D_{BP} = 0.848$	$D_{BP} = 0.795$
$D_{Si} = 0.916$	$D_{Si} = 0.897$
$E_{1/D} = 0.699$	$E_{1/D} = 0.571$
$H' = 2.64$	$H' = 2.45$
$J' = 2.28$	$J' = 1.98$
$D_{MI} = 0.833$	$D_{MI} = 0.794$
$E_{MI} = 0.937$	$E_{MI} = 0.897$
	$GC = 0.395$
	$CH = 2.66$
	$STVI = 0.826$

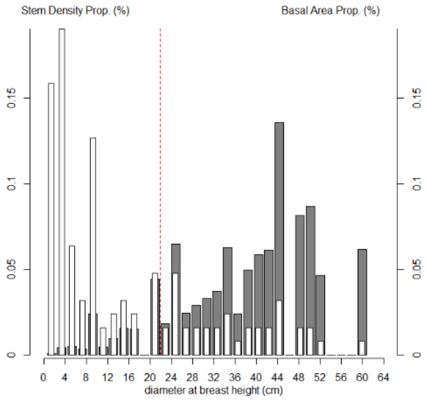
(c) uniform / irregular



$D_{Mg} = 4.37$	$D_{Mg} = 4.80$
$D_{Mn} = 2.75$	$D_{Mn} = 3.22$
$D_{BP} = 0.897$	$D_{BP} = 0.764$
$D_{Si} = 0.928$	$D_{Si} = 0.875$
$E_{1/D} = 0.821$	$E_{1/D} = 0.471$
$H' = 2.72$	$H' = 2.37$
$J' = 2.45$	$J' = 1.87$
$D_{MI} = 0.872$	$D_{MI} = 0.797$
$E_{MI} = 0.967$	$E_{MI} = 0.854$
	$GC = 0.475$
	$CH = 2.27$
	$STVI = 0.908$

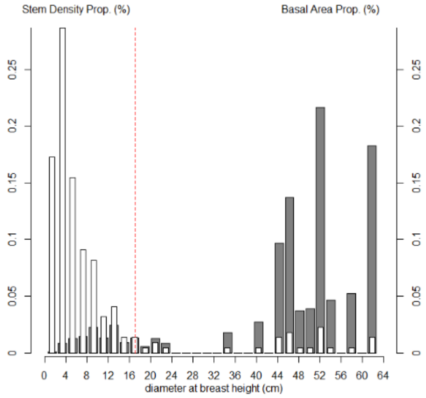
Figure 3. Example values of indicators in Table 1 obtained for diverse forest structural types.

(d) reverse J / balanced



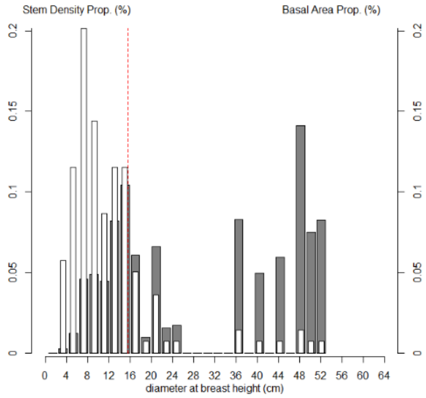
Unweighted $p_i = n_i/N$	Weighted $p_i = g_i/G$
$D_{Mg} = 5.17$	$D_{Mg} = 6.89$
$D_{Mn} = 2.32$	$D_{Mn} = 4.23$
$D_{BP} = 0.810$	$D_{BP} = 0.864$
$D_{Si} = 0.906$	$D_{Si} = 0.936$
$E_{1/D} = 0.410$	$E_{1/D} = 0.598$
$H' = 2.77$	$H' = 2.92$
$J' = 1.85$	$J' = 2.05$
$D_{MI} = 0.761$	$D_{MI} = 0.891$
$E_{MI} = 0.863$	$E_{MI} = 0.928$
	$GC = 0.728$
	$CH = 1.39$
	$STVI = 0.681$

(e) peaked reverse J / regenerated



$D_{Mg} = 3.89$	$D_{Mg} = 5.67$
$D_{Mn} = 1.48$	$D_{Mn} = 3.46$
$D_{BP} = 0.714$	$D_{BP} = 0.784$
$D_{Si} = 0.845$	$D_{Si} = 0.881$
$E_{1/D} = 0.293$	$E_{1/D} = 0.381$
$H' = 2.25$	$H' = 2.48$
$J' = 1.54$	$J' = 1.72$
$D_{MI} = 0.650$	$D_{MI} = 0.776$
$E_{MI} = 0.770$	$E_{MI} = 0.832$
	$GC = 0.864$
	$CH = 1.17$
	$STVI = 0.161$

(f) bimodal / two-cohort / recruitment



$D_{Mg} = 3.45$	$D_{Mg} = 5.56$
$D_{Mn} = 1.53$	$D_{Mn} = 3.90$
$D_{BP} = 0.799$	$D_{BP} = 0.859$
$D_{Si} = 0.884$	$D_{Si} = 0.922$
$E_{1/D} = 0.477$	$E_{1/D} = 0.712$
$H' = 2.36$	$H' = 2.67$
$J' = 1.81$	$J' = 2.23$
$D_{MI} = 0.720$	$D_{MI} = 0.920$
$E_{MI} = 0.862$	$E_{MI} = 0.943$
	$GC = 0.658$
	$CH = 1.54$
	$STVI = 0.780$

DBH distributions (white bars) and basal area-weighted (grey bars); dashed line: QMD

Staudhammer and LeMay (2001) suggested comparing empirical weighted DBH variances against three theoretical distributions – uniform (maximum entropy) and maximally bimodal (maximum variance) – also in relation to a situation of absolute equality between all tree DBHs (minimum variance and entropy). Although the relevance of comparison against a theoretical uniform distribution is more profoundly discussed below (Section 3.2.2), it is worth noting at this point that the above-mentioned FSTs can be separated into two groups according to whether their weighted DBH variances are lower – even-sized, re-initiation, uniform – or higher – reverse J, bimodal – than that of a theoretical uniform distribution. If only this division is taken into account (compare cold versus warm colours in Fig. 4[11]), then the relationships found for most indices may become more consistent. It can be seen, for instance, that the unweighted Shannon index arranges even-sized and uniform plots in a logical manner, and thus these inconsistencies are only shown if more complex FSTs occur in a given forest ecosystem, or under a certain management regime like the shelterwood method involved in this doctoral thesis. In such cases, an optimisation method based on Shannon diversity could simply result in local optima (Önal 1995).

As a consequence, there are cases for which Shannon shall be used, but its indiscriminate use, without careful checks of its meaning and significance, may easily result in misleading conclusions. Using Shannon and other entropy-based indices requires a method to assure comparability among the forests types in study. Intrinsic diversity and equitability ordering are the diagnosis tools that have to be employed to ensure that the assumptions underlying these indices are not violated (Section 2.2). Results in Study I also showed that a more straightforward method could be employed by simply ensuring that comparisons are carried out within the above-mentioned groups – either even-sized or uniform, or reverse J and bimodal – and never mixing forest structures between these groups. This can be achieved by simply checking that all empirical variances are either higher or lower than the variance of a theoretical uniform (Staudhammer and LeMay 2001). This is the case, since the uniform distribution defines the type of DBH distribution of maximum entropy[12] (Önal 1997b), whereas reverse J shapes provide the highest ecologically-plausible DBH variances (signified along the x-axis in Figs. 4).

Study I also showed that a similar approach can be carried out using the Gini coefficient, as it asymptotically takes the value of $GC = 0.5$ for a uniform distribution. Figure 4 illustrates how this value defines a clear boundary between these two groups. This is yet another argument for supporting the use of GC above all the other indicators in Table 1, as an indicator of concentration (relative dispersion) along its range which may also be used for evaluating entropy (knowing that $GC = 0.5$ signifies maximum entropy, while $GC = 1$ is maximum dispersion). This was signified in the dynamics observed in Study V: Fig. 1, which showed how seed regeneration after forest disturbance leads to a shift in GC from the lowest value to the highest. This is because, from a situation of low entropy stabilized by self-thinning, forest disturbance and subsequent seed regeneration prompts an abrupt increase in DBH dispersion while not in entropy, as ingrowth takes place. This is the reason Barbeito et al. (2009) also found a discrepancy in their Shannon measurements due to regeneration fellings, in a study carried out in that same study area (Valsaín).

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[11] Note that similar colouring has been consistently followed in subsequent figures, also coinciding with those used for the article in Study V.

[12] Observe that close-to-uniform distributions obtained the highest unweighted values for Simpson and Shannon in Fig. 4

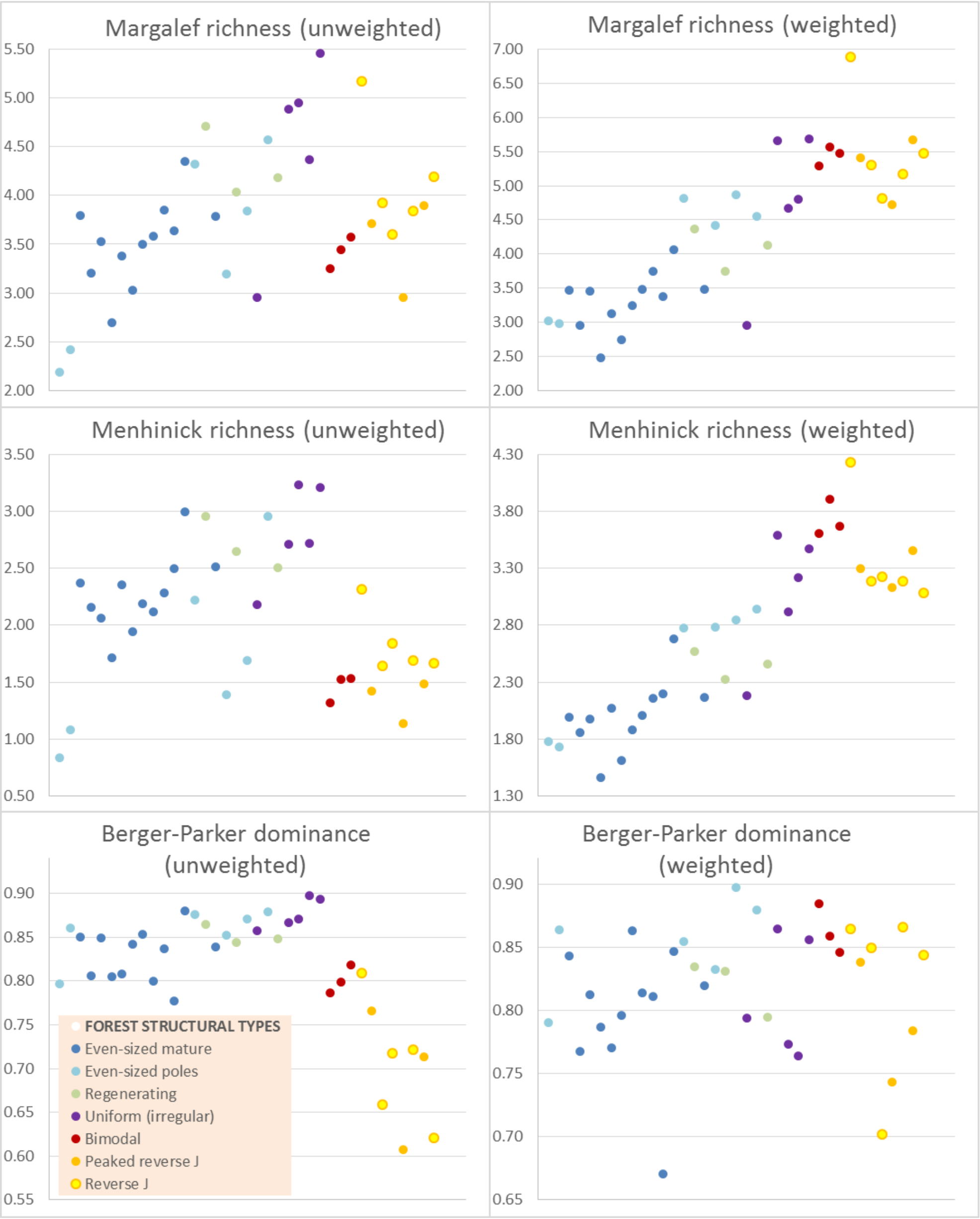

Figure 4. Values of indicators in Table 1. Forest plots arranged by increasing DBH variance on the x-axis.

Figure 4. Values of indicators in Table 1. Forest plots arranged by increasing DBH variance on the x-axis.

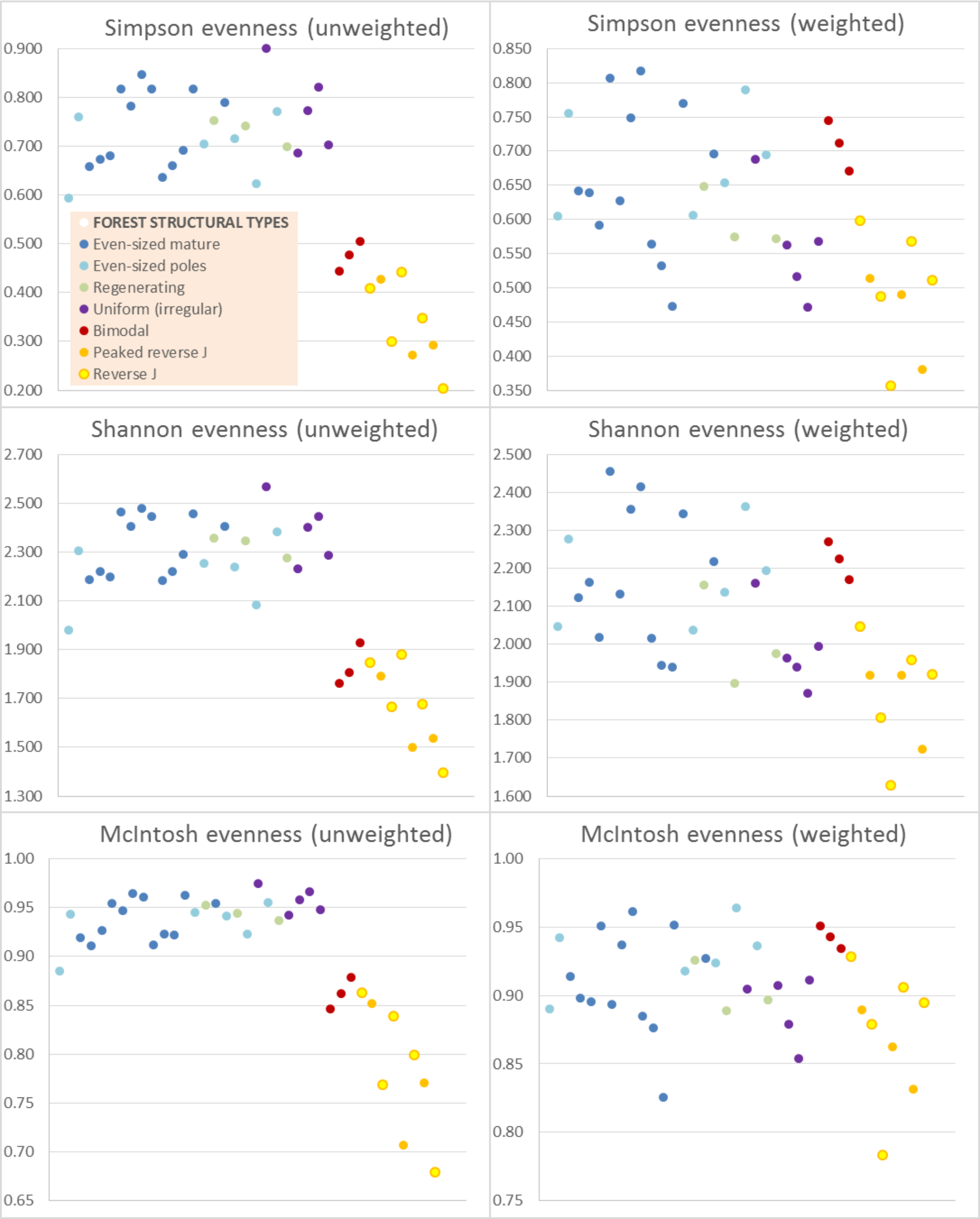

Figure 4. Values of indicators in Table 1. Forest plots arranged by increasing DBH variance on the x-axis.

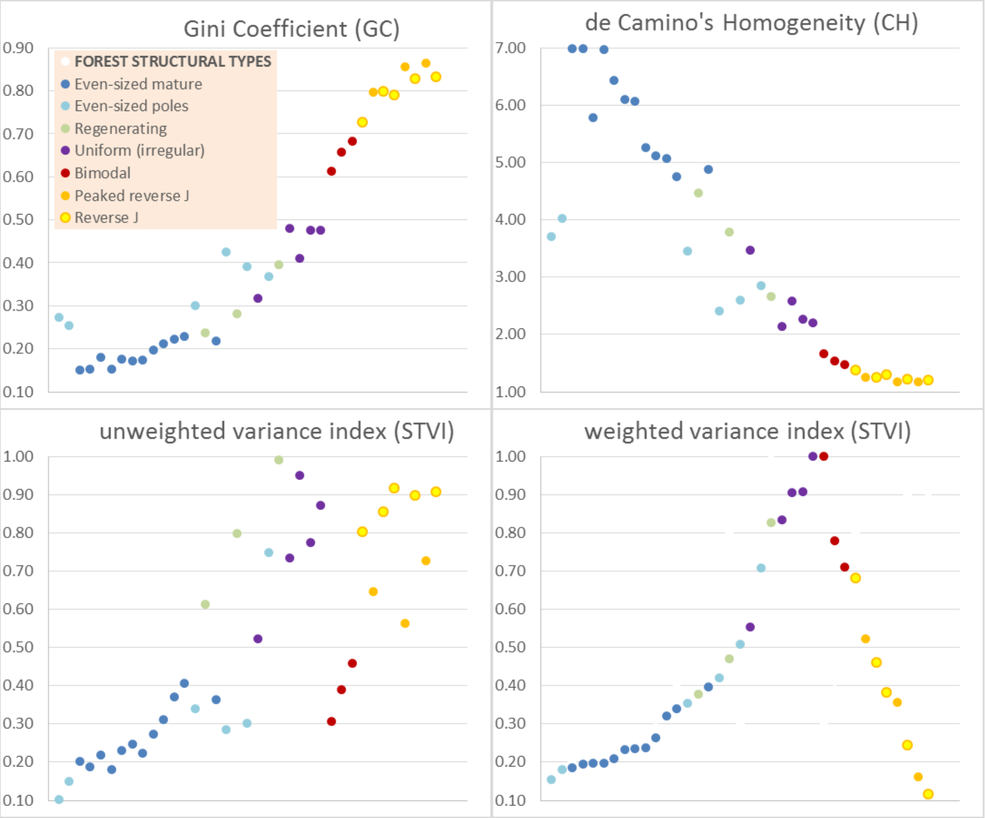

Figure 4. Values of indicators in Table 1. Forest plots arranged by increasing DBH variance on the x-axis.

3.1.2 *The cause: even and uneven-sized forests lack intrinsic ordering, violating the assumptions of diversity and equitability indices.*

As detailed in Section 2.2, we selected the majorization method (Solomon 1979) to test the intrinsic diversity $I_k(k, M_k)$ and equitability $P_k(x_k, M_k)$ ordering observed between all the field plots to be compared by indices of richness, diversity and evenness in Table 1. Although the diagnosis of these profiles was performed by pair-wise comparison of population samples, this doctoral thesis shows the diversity (Fig. 5) and equitability (Fig. 6) profiles for all the plots altogether. Upper plots (a-b) represent profiles computed from unweighted abundances, while lower plots (c-d) were basal area-weighted. Similarly, plots on the left (a,c) represent intrinsic ordering, whereas those on the right (b,d) are profiles of diversity (Study I: Eq. 5) and equitability numbers (Study I: Eq. 9). Both can be used for diagnosis, but they are conceptually different. Intrinsic ordering is used to test compliance with the assumption underlying a method based on the theory of information (Lambshead et al. 1983): they indicate the *cause*. Diversity and equitability profiles simply represent a number of indices related by parametric generalised entropy (Study I: Eq. 4) as a continuum (Patil and Taillie 1977), therefore signifying the inconsistencies found (Section 3.1.1). In other words, they are the *consequence*. Thus, intrinsic ordering (a-b) is employed to determine whether the abundance distributions compared are consistent with the definition of diversity, as an assumption to be tested whenever diversity and equitability indices are employed. It was also demonstrated in Section 2.2 and Study I that they relate directly to the Lorenz curve. On the other hand, diversity and equitability profiles (b,d) are better employed to select the more suitable index for a given problem in hands, whether rarity, richness or dominance is more suited to explain the relationships found in each case.

Under the diversity scale given by majorization (Figs. 5a,c) a forest plot has greater diversity of size classes than another if its intrinsic diversity ordering $I_k(k, M_k)$ lies completely below. Generally speaking, profiles were comparable when they originated from similarly-shaped distributions. It can be seen in Fig. 3 and Fig. 2 of Study I that a balanced reverse J would always have more diversity of DBH classes than a peaked reverse J. Both are comparable as their unweighted and basal area-weighted DHB distributions have similar shapes. Many other profiles intersected, however, indicating that two given populations are non-comparable using this diversity scale. Profiles from even-sized plots intersected those from reverse J-shaped ones, indicating that they are non-comparable. Forest areas approximating a uniform distribution present a particular case that is key to deciding whether relative abundances are to be weighted or not. They can be compared to even-sized if unweighted, but only to reverse J shaped structures if weighted, due to the very different shapes of their unweighted and basal area-weighted DBH distributions. The outcome is are the confusing values obtained in Figure 4.

Figures 5b,d are the diversity numbers (N_α) demonstrating whether diversity indices order them logically and consistently. The grey boxes in the background of these figures illustrate the correspondence between the order of entropy (α) and the diversity indices described (see Study I: eq. 4), which are explicitly indicated at the bottom of the grey boxes. Entropy of order $\alpha = 0$ is the number of DBH classes $S = N_0 = e^{H_0}$, and thus explains the concept of *richness*. The other two concepts involved in diversity are *dominance* and *rarity*[13], represented in diversity profiles by $\alpha \to \infty$ (to the right) and $\alpha \to -\infty$ (to the left), respectively (Hill 1973). It can be confirmed that $D_{BP} = N_\infty$, as it emphasises the proportion of the most dominant DBH class. An unweighted index of pure rarity was also applied by Buongiorno et al. (1995) who employed the minimum number of trees in any DBH class ($n_{\min}$)[14], which can therefore be defined as $N_{-\infty}$ in the context of generalised diversity numbers. Values between these extremes are measures taking into account several of these concepts simultaneously. Entropy of order $\alpha = 1$ equals Shannon's $H' = \ln(N_1) = H_1$; and the entropy of order $\alpha = 2$ is described in Simpson's index $D_{Si} = N_2 = e^{-H_2}$. Consequently, Simpson is more influenced by dominance and Shannon by rarity and richness. The intersecting curves in Figs. 5b,d demonstrated that S, $H^{'}$, D_{Si}, and D_{BP}, categorised the plots inconsistently by their structural diversity, and they cannot be relied upon to provide a logical order of the empirical plots according to their structural complexity.

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[13] Which are simultaneously expressed in Shannon's index as relative abundance (p_i) – the dominance of a DBH class – and surprisal ($-\ln p_i$) – its rarity – (Gove et al. 1994).

[14] If expressed as relative abundances, $N_{min} = n_{\min}/N$, it compares directly to Lexerød and Eid's (2006) version of the Berger-Parker index (Table 1).

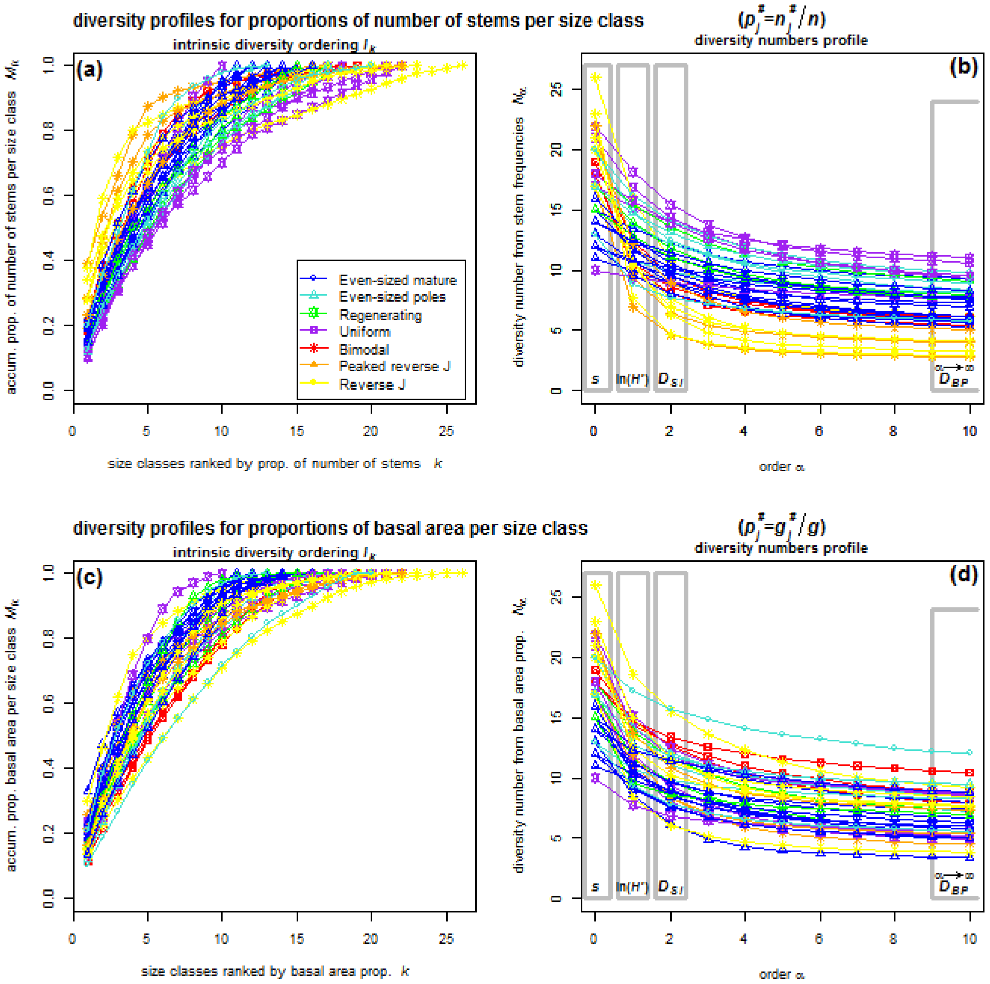

Figure 5. Diversity profiles.

Similarly, Figs. 6b,d are the equitability numbers ($E_{\alpha,0}$) obtained by these plots, and therefore they illustrate whether evenness indices, i.e. the diversity numbers normalised by richness, order them logically and consistently. The correspondence with the indices derived from generalised entropy is also shown in the grey boxes in the background of these figures. Most results were consistent, and there were only small differences between J' and E_{Si} ($\alpha = 1$ and 2, respectively) for those plots lacking intrinsic ordering. Unweighted versions showed clearer differences between even and uneven-sized plots than weighted ones (see also evenness indices in Fig. 4).

Figs. 6a,c show the intrinsic equitability ordering $P_k(x_k, M_k)$, their Lorenz ordering by DBH classes. The grey diagonal line represents the ideal situation in which abundances are equal between all the DBH classes present within that tree population. Curves closer to the diagonal therefore signify greater equitability between DBH classes: i.e. more entropy.

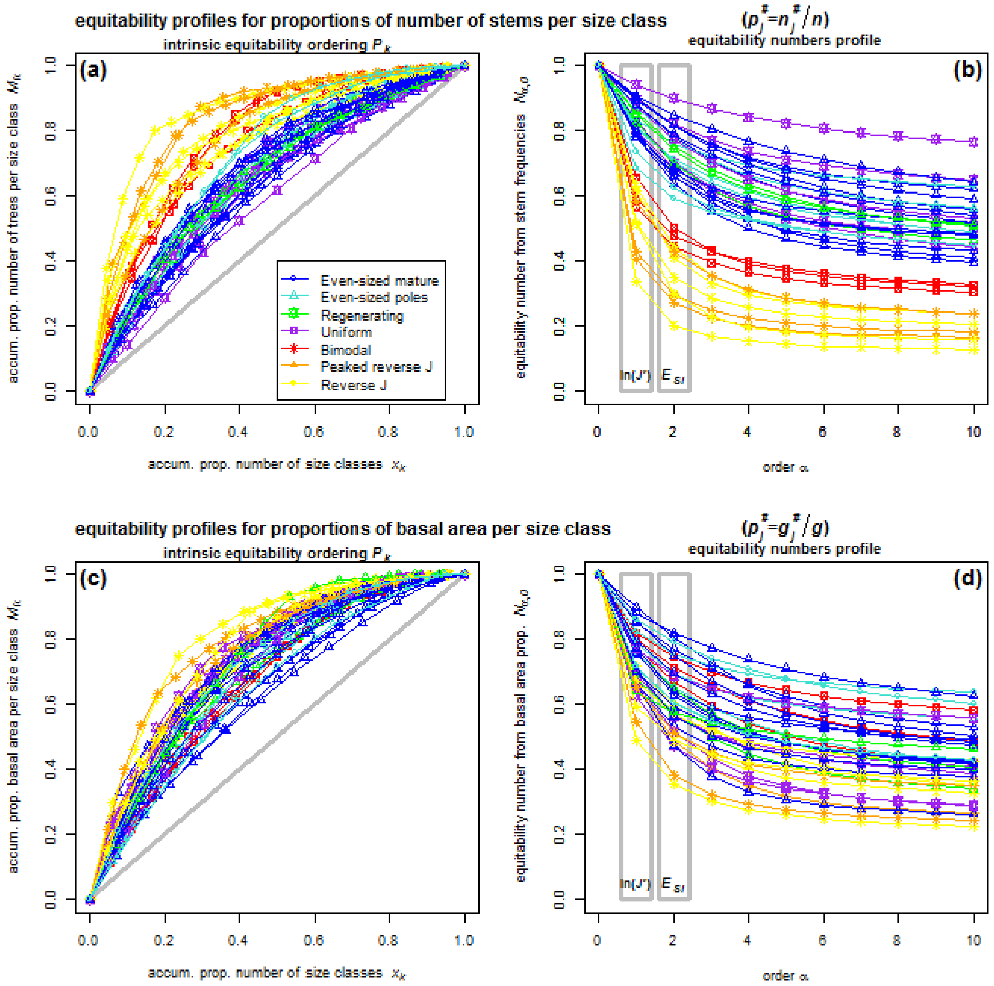

Figure 6. Equitability profiles.

Profiling equitability resulted in fewer intersections than diversity, and spacing between curves was more evident. Many intersecting intrinsic equitability profiles were also detected, however. In particular, bimodal structures seemed to be a difficult case, non-comparable by most of the methods outlined in Table 1. Consequently, there is a need to accompany the indicators by a measurement of asymmetry. This issue was later discussed and implemented in the context of the Lorenz curve's analysis (Section 3.2.4).

Section 2.2 showed the link between majorization and the Lorenz ordering for the exact case of studying entropy between DBH classes, also reflecting on how those same equations led to a consideration of the computation of Lorenz curves from single tree information (eqs. 2-3). Figure 7 shows the Lorenz curves obtained when trees were ranked individually $L_r(x_r, M_r)$. The relationships in these curves were clearer, and they allowed characterisation of the dynamics due to the type of shelterwood management applied in the study area. Lorenz curves generated from individual trees clearly showed the best separability among FSTs. Study I developed these ideas into an argument that measuring individual tree DBH

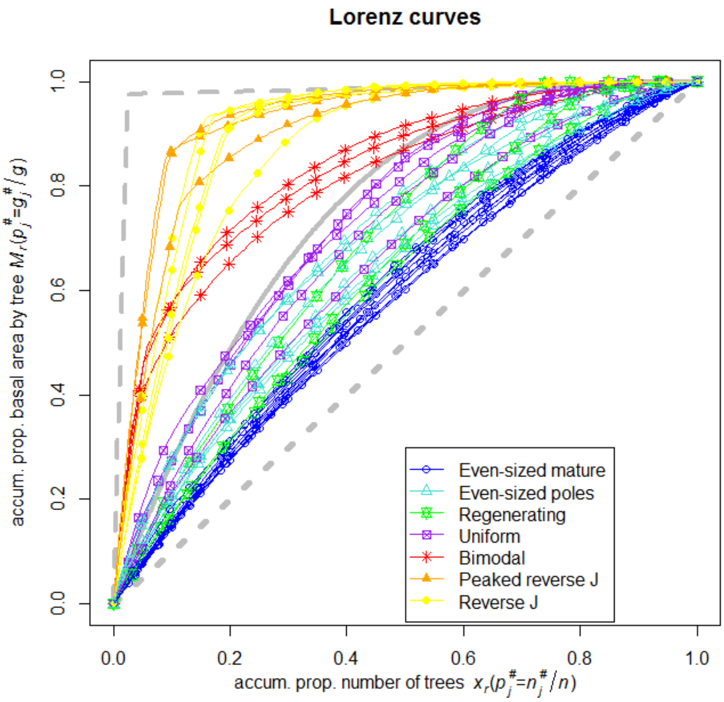

Figure 7. Lorenz curves

inequality is more correct than evaluating entropy between DBH classes. As a consequence, all the indicators from Table 1 which were based on the theory of information were ultimately dismissed from further research (Studies II-VI), as will be explained below, focusing this doctoral thesis on the study of the Lorenz curve of tree size inequality and its relationship with ALS remote sensing.

It must also be acknowledged that there could be a number of, perhaps more sophisticated, statistical approaches to pursuing the hypotheses of Study I. Future research on intrinsic ordering should make use of statistical inference. Lack of bias and consistency of abundance vector estimators can be only assured using replicated samples (Barabesi and Fattorini 1998). Richness estimators are only asymptotically unbiased, and therefore inference from finite samples should make use of rarefaction (Magurran 2004; Legendre and Legendre 2012) or jack-knife procedures (Gove et al. (1994) did this for intrinsic diversity ordering and Dixon et al. (1987) for Lorenz ordering). These are especially necessary when the assumption of random spatial distribution of stems[15] is not met (Barabesi and Fattorini 1999). The jack-knife procedure was, however, only conceived as an approximate test (Gove et al. 1994). More complex simultaneous inference was further developed for parametric (Fattorini and Marcheselli 1999) and non-parametric (di Battista and Gattone 2003) estimation of confidence intervals of intrinsic profiles obtained from samples, and using them in hypothesis testing. These actually apply to all the methods involved in this doctoral thesis: intrinsic diversity and equitability ordering and Lorenz curves.

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[15] In their horizontal structure, sensu Section 1.2

3.1.3 The consequence: ALS metrics fail to explain variability for most indicators.

The next step was to carry out an exploratory analysis in pursue of Objective 2a of this doctoral thesis: study the relationship that ALS metrics may have with the targeted indicators, selecting those which can be accurately obtained with ALS remote sensing (Section 1.4). Although the scope of Studies II and III were narrowed to the relationships of ALS with the Lorenz curve and derived indicators, there was also a first screening targeted at the entire assortment of indices pointed out in Table 1. Correlations with all the ALS predictors were systematically computed for all the indicators in study, including the variable transformations specified in Table 2. A selection of the most relevant results is listed in Table 3.

The results showed that there would be little hope of establishing a relationship between ALS metrics and diversity indices. Paradoxically, ALS seemed to have more potential for predicting diversity measured from weighted abundances, which are precisely those that were rendered most useless by results in Study I (see Fig. 4). More in line with previous results, evenness indices showed better correlations with most ALS metrics than their diversity counterparts. Although indices based on equitability of unweighted abundances indeed showed some degree of correlation, those based on the Lorenz ordering and also indicators describing richness (Margalef and Menhinick) were much more related to ALS metrics. This could be an indication that they are truly related to the physical structure of biomass material in the forest's vertical profile. There was no further investigations involving richness indices, since methods based on Lorenz ordering were found superior to those involving entropy. Nonetheless, Fig. 4 illustrates the usefulness of these indicators when weighted (which in this case it means basal area-normalised richness, see Table 1). Particularly, Menhinick's index was regarded as being especially appropriate, as Fig. 4 shows how the group of even-sized structures was completely separated from the remaining FSTs. Ironically, to my knowledge, this doctoral thesis has been the first research study to include Menhinick's index among those outlined in Table 1. Richness indices have not been popular with authors measuring structural diversity, at least not for those cited in Section 1.2.1, and only Lexerød and Eid (2006) included Margalef's index among those they compared, while FORESTEUROPE considered structural diversity by the number of DBH classes (Ståhl et al. 2011). In my opinion, if further opinions are to be given on the theory of information applied to DBH classes, at least richness and equitability should be evaluated separately from diversity.

From the results in Table 2, it could be deduced that ALS has little capacity for explaining variance in these indicators. One conclusion that could perhaps be reached is that ALS remote sensing would fail to detect key features describing structural complexity, and therefore be unsuitable for predicting these indicators. However, I consider lidar-based remote sensing methods in forest science as an alternative to measuring and sampling like any other (Maltamo et al. 2014: 64, 269). ALS in particular has a great amount of uncertainty in forest mensuration, compared to field methods, although less than other remote sensing methods. It is also certainly the most suited for forest structure characterisation (Latifi 2012). My opinion is that the fact that some indicators show little relation to ALS metrics is not caused by the incapacity of ALS to measure them, but is more related to the incapacity of those indicators to actually describe the physical properties of that forest, or doing so in a way that yields a logical ranking (Lexerød and Eid 2006). From my point of view, non-significance in Table 3 thus adds further evidence for dismissing those indicators and favouring the ones showing actual relationships with ALS datasets and the FSTs themselves.

Table 3. Correlations of indices (rows) against a selection of ALS metrics (columns). Their relationship to weighted DBH variance is shown as well. ALS metrics are described in the appendix.

ALS metrics	*Mean*	*Mode*	*SD*	*CV*	*Skew*	*Kurt*	*P50*	*P75*	*P90*	*Max*	*Count*	*Cover*
Margalef index (D_{Mg})												
Unweighted	-.12	.01	.18	.14	-.25	-.23	-.19	-.05	-.07	-.10	-.22	-.26
Weighted	-.65	-.38	**.73**	**.76**	-.66	-.62	-.69	-.50	-.34	-.32	-.55	.22
Menhinick index (D_{Mn})												
Unweighted	.26	.20	-.27	-.31	.14	.15	.17	.21	.13	.11	.04	-.64
Weighted	**-.73**	-.49	**.78**	**.86**	**-.70**	-.66	**-.80**	-.62	-.40	-.35	-.64	.11
Berger–Parker index (D_{BP})												
Unweighted	.02	.03	-.52	-.34	.05	.13	.11	-.13	-.21	-.18	.04	-.25
Weighted	-.29	-.07	.10	.19	-.28	-.29	-.17	-.31	-.23	-.17	-.19	.33
Simpson index (D_{Si})												
Unweighted	.01	.01	-.45	-.29	.02	.12	.07	-.11	-.19	-.17	.01	-.25
Weighted	-.37	-.12	.18	.30	-.34	-.33	-.23	-.38	-.26	-.22	-.27	.41
Simpson evenness ($E_{1/D}$)												
Unweighted	.46	.22	-.49	-.50	.50	.46	.46	.33	.27	.27	.36	-.30
Weighted	.47	.23	-.54	-.54	.51	.48	.47	.34	.26	.26	.37	-.36
Shannon index (H')												
Unweighted	-.15	-.07	-.20	-.09	-.18	-.10	-.10	-.18	-.28	-.27	-.16	-.16
Weighted	-.46	-.19	.34	.44	-.45	-.41	-.36	-.42	-.30	-.28	-.33	.41
Shannon. evenness (J')												
Unweighted	.34	.18	**-.70**	-.61	.35	.37	.39	.18	.02	.04	.23	-.45
Weighted	.08	.07	-.42	-.25	.17	.19	.25	-.11	-.04	.00	.12	.10
McIntosh index (D_{MI})												
Unweighted	.25	.16	-.54	-.47	.22	.26	.26	.12	.01	.02	.12	-.54
Weighted	-.65	-.41	.44	.62	-.56	-.53	-.56	-.67	-.41	-.32	-.54	.21
McIntosh evenness (E_{MI})												
Unweighted	.22	.12	-.65	-.51	.25	.30	.29	.06	-.06	-.04	.17	-.37
Weighted	-.08	.02	-.24	-.08	-.01	-.01	.11	-.22	-.13	-.07	-.02	.23
Gini coefficient (GC)												
Weighted	-.55	-.31	**.89**	**.80**	-.58	-.61	-.67	-.35	-.18	-.16	-.49	.24
de Camino homogeneity (CH)												
Weighted	.69	.42	**-.78**	**-.77**	**.71**	**.73**	**.75**	.54	.41	.34	.60	-.24
Structure index based on variance ($STVI$)												
Unweighted	-.18	.02	.56	.39	-.35	-.42	-.37	-.01	.01	.02	-.32	-.24
Weighted	-.55	-.38	.30	.49	-.47	-.42	-.53	-.60	-.39	-.31	-.55	-.22
Basal area-weighted DBH variance (s^2_{DBH}) (Table 1)												
Weighted	-.39	-.17	**.89**	**.74**	-.47	-.52	-.56	-.18	.00	.00	-.40	.17

Mean: mean of ALS heights.
Mode: mode of ALS heights.
SD: standard deviation of ALS heights.
CV: coefficient of variation of ALS heights.
Skew: skewness of ALS heights.
Kurt: kurtosis of ALS heights.
P50: median of ALS heights.
P95: 95th percentile of ALS heights.
P99: 99th percentile of ALS heights.
Max: maximum of ALS heights.
Count: number of ALS heights.
Cover: proportion of ALS heights above 1m.

Dispersion (Inequality) versus Entropy

The most important lesson that can be learned from the relationship between ALS metrics and the indicators is that the physical properties recorded by backscattered lidar pulses are more related to DBH dispersion (concentration) than to entropy between DBH classes. It may therefore be inferred that differences in forest structure are better described by the concept of inequality than by entropy. There would thus be an actual relationship of causality between the distribution of ALS returns and indicators based on dispersion, while no cause-effect can be deducted from indicators describing entropy. Using entropy to describe forest structure may therefore be conceptually wrong. This could be the grounds for the inconsistencies found in indicators based on theory of information. Many authors have based forest management on the concept of entropy (e.g. Buongiorno et al. 1995; Solomon and Gove 1999; Önal 1997a; see review by Hyytiäinen and Haight 2012) and there is therefore a number of reasons to employ it as a reference scale. It makes sense to compare forest structures by their entropy as, for instance, Study V showed how seed regeneration after disturbance leads to a quick shift in dispersion (from green to yellow lines in Fig. 7), without involving much change in entropy (same lines in Fig. 6c). This is the reason why values of diversity indices are similar for reverse J and even-sized structures, since they are actually rather close in terms of entropy. They are very dissimilar, however, with regard to their DBH dispersion.

Perhaps the easiest way to conceptualise the difference between dispersion and entropy is to observe the Lorenz ordering plots. Figures 6a,c establish a scale of entropy between DBH classes from the diagonal, which marks the situation of maximum entropy. On the other hand, Fig. 7 establishes a scale of increasing dispersion from the diagonal, with maximum dispersion represented by the maximal bimodal (dashed grey line). I suggest that a scale of entropy may also be conceptualised from the Lorenz curves in Fig. 7, as the curve denoting the theoretical uniform distribution denotes the condition of maximum entropy. From this line, entropy decreases in either direction. Thus, my opinion is that the Lorenz curves in Fig. 7 and derived indicators should be used for diagnosis of either dispersion or entropy, as desired for each case. In the particular case of GC, dispersion or inequality is assessed as an increase toward its maximum value at $GC = 1$, whereas entropy can be evaluated as the distance to the value of maximum entropy at $GC = 0.5$. Staudhammer and LeMay's (2001) $STVI$ is a particular type of index which transforms the scale of dispersion, given by the weighted DBH variance[16], to express entropy instead. This is the reason why its relationship to ALS metrics has been as poor as those obtained for diversity indices. It is, however, a neat idea to employ an index based on a dispersion measurement and use it to denote entropy. It is thus recommended above other indices describing entropy, as it complies with the Lorenz ordering and simply establishes an increase toward the situation of maximum entropy. A similar approach has been suggested by Önal (1997b), although his index has been rarely applied in the literature. On the other hand, richness indices also obtained relatively high correlation values with the ALS metrics. This stresses the relationship between richness of DBH classes and DBH dispersion, as the former basically describes the dispersion of tree sizes amongst many different DBH classes. This is probably the reason that Margalef and Menhinick's indices have shown similar properties as those of Gini and de Camino (Fig. 4).

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[16] Although Staudhammer & LeMay (2001) conceived their index from a weighted variance (Table 1), we considered the possibility of computing it from an unweighted variance as well (Fig. 4), for which this property nevertheless remains invariable.

Variable transformations and model selection

Little improvement was observed in the relationship between ALS metrics with the target indicators when carrying out variable transformations. Most diversity and evenness indices would benefit slightly from a logarithmic transformation in the response. This does not apply to Shannon which is already expressed in a logarithmic scale (see Figs. 5-6b,d), as a consequence of the inclusion of surprisal ($-\ln p_i$) in its formula, to express rarity (Gove et al. 1994). Perhaps, exponential or multiplicative models (Table 3) would therefore be desired for most of these indicators. The improvement is, however, small compared to the linear model, and a final decision may also depend on other criteria. In general, I would say that Table 3 shows no significant improvements for most of the indicators.

A more obvious case pertains to the distribution of de Camino's homogeneity index (CH). Exponential and multiplicative models (Table 2) seemed to improve the relationships of this indicator with many of the most relevant ALS metrics. Conversely, it can be easily seen from Fig. 4 that the empirical values of this indicator are already distributed in a logarithmic scale. Thus, I would recommend applying an inverse logarithm (sigmoid curve) transformation in the response itself. In other words, I would suggest modifying the original index (Table 1) into $CH = \ln(\sum_{k=1}^{N}[(n_{\leq k}/N) - (g_{\leq k}/G)]/\sum_{k=1}^{N}(n_{\leq k}/N))$. The logarithmic transformation would regulate the scale across its dynamic range, so that differences between populations are more equally assessed among all types of structures. It would also constrain its values within the [0,1] range. The inverse transformation would simply transform it into a "heterogeneity" index, instead of the original "homogeneity", increasing for higher tree size inequality. The outcome would yield very similar properties as GC.

Although it is true that, as an indicator of entropy, $STVI$ shows little relationship to the distribution of ALS returns, there are still methods to achieve a reliable remote sensing-assisted prediction. It is worth mentioning that the weighted DBH variance from which $STVI$ derives does show clear relationships with ALS metrics (correlations were included at the bottom of Table 3, along with the indicators). The correlations obtained are comparable to those for GC. Moreover, they are also mainly related to descriptors of dispersion in ALS heights. The case thus seems clear: ALS dispersion relates to DBH dispersion. If the original intention for which authors have focused on describing entropy is still a requirement, e.g. for pursuing specific forest management objectives (Gove et al. 1994, 1995), then the key would be to define how the situation of maximum entropy can be characterised from ALS datasets. This doctoral thesis further focused on completing this task using the Lorenz curves (Study V).

Apportioning by height classes or weighting by volume or above-ground biomass provided no significant improvement

The inclusion of a height component in the response was presumed to add an advantage with regards to ALS estimation, since it may be more intuitively postulated that ALS heights would have a causal relationship to tree heights than to tree DBHs. The research carried out for this doctoral thesis involved two ways of including height information in the indicators outlined in Table 1. One approach was to apportion the data in height classes instead of DBH classes, measuring vertical differentiation as per MacArthur and MacArthur (1961). The other approach was weighting relative abundances by volume or above-ground biomass, whose allometry included individual tree height as a predictor. A third alternative that was also implemented was a combination of both, accounting for relative proportions of volume and biomass by height classes. Contrary to the prior presumption, none of these approaches yielded a significant improvement. This was surprising, as ALS is usually fairly better related to forest parameters expressing height than those related to basal area (e.g., Næsset 2002; Maltamo et al. 2014: 219). This result, however, actually makes sense, since what is being measured is variation in height or basal area, which must nevertheless be very similar and therefore show a similar relationship to ALS metrics. I have therefore omitted detailed reports of those results from this doctoral thesis, as no relevant additions were deduced. The properties of indicators were very similar to those found for basal area-weighted abundances, and relationships with ALS metrics did not significantly improve either.

The research carried out afterwards also showed many advantages in using basal areas. While volume or above-ground biomass depend on allometry, the quadratic relationship between DBH and basal area yielded desirable mathematical properties, such as clearly situating the position of the QMD along the Lorenz curve (see Study V and Section 3.2.3). Nonetheless, a possibility for further research would be to determine whether similar mathematical properties would also stand for volume by using the theory of size-biased distributions of third order. Gove (2003), however, doubted this would have a practical use in forestry.

3.1.4 Rounding off: unsuitability of diversity indices for forest structure characterisation

After considering many possibilities for describing the structural complexity of forests, all of which were available in the scientific literature (Table 1), Study I demonstrated that indices based on the theory of information (e.g. diversity indices) were unsuited for such purposes, by using a deeper insight in the mathematical theory of diversity and equitability ordering. These results contradicted the rather widespread use in the literature of entropy-based indices for evaluating forest structure (e.g., MacArthur and MacArthur 1961; Murdoch et al. 1972; Willson 1974; Aber 1979; Erdelen 1984; Buongiorno et al. 1994; Gove et al. 1994; Pretzsch 1995; Ferris-Kaan et al. 1998; Lähde et al. 1999b; Berger and Puettmann 2000; Wikstrom and Eriksson 2000; Staudhammer and LeMay 2001; Sullivan et al. 2001; del Río et al. 2003; Harper et al. 2003; O'Hara et al. 2004; Rouvinen and Kuuluvainen 2005; Lexerød and Eid 2006; Sterba and Zingg 2006; McRoberts et al. 2008; Lei et al. 2009; Pretzsch 2011; von Gadow et al. 2012; Ozdemir and Donoghue 2013). The fact that very different stand structures may obtain similar values of Shannon indices was detected by Buongiorno et al. (1995) at an early stage, but has remained largely overlooked for years. The incapacity of diversity indices to provide a logical ranking of the populations compared under certain conditions, and the approach to solving this contingency by profiling intrinsic diversity and equitability has been long-discussed in the fields of ecology and biodiversity (Hulbert 1971; Lambshead et al. 1983), but is relatively new to forestry and forest structure characterisation. Although Gove et al. (1992, 1995) employed intrinsic diversity ordering for evaluating forest structural complexity, concise indices based on entropy have been further applied without careful checks of the assumptions underlying them. The results presented in this doctoral thesis showed that these indices are inadequate for comparing forest structural types which are situated at different sides of the $GC = 0.5$ threshold (which defines maximum entropy). I discourage therefore any further use of indicators based on the theory of information that do not include an analysis of intrinsic ordering. Lexerød and Eid (2006) reached similar conclusions, although using a heuristic approach based on inductive exploratory multivariate analysis and practical criteria (discriminant ability and capacity to provide a logical ranking). The major contribution of this research is in introducing a deductive approach based on mathematical demonstration that settles the question of the inadequacy of diversity and equitability indices for forest structure characterisation.

One of the reasons the properties revealed by this research may have remained unnoticed by other authors could be that it is uncommon to apply no lower DBH limit when recording the trees in the plot, as we did in this study, therefore including saplings and seedlings (details on the field mensuration protocol are provided in Study II and Valbuena et al. 2012). This may pose a problem regarding the practical applicability and pan-European implementation of the methods developed, as it is common practice to impose a DBH threshold under which no tree data is recorded from field samples (a merchantability limit or alike). Two strategies could be followed to overcome this difficulty: (1) employ modelling techniques to estimate regeneration and recruitment from truncated DBH distributions, or (2) develop ALS-based methods not requiring calibration from field data. Further research is therefore needed to analyse the real effect that using truncated data could have in these results, as well as on the noted approaches to overcoming it.

The results presented in this thesis and Study I, however, do not necessarily invalidate the above-mentioned research contributions. Diversity and equitability indices are also perfectly valid if the forests compared are all either $GC \geq 0.5$ or $GC < 0.5$, i.e. their variances are larger or smaller than a theoretically uniform distribution, respectively (cf. de Camino 1976; Staudhammer and LeMay 2001). Thus, diversity indices can be employed for stand structure comparisons if the forests contrasted are all either even-sized or uneven-sized (e.g. Buongiorno et al. 1994). In any case, the validity of studies based on theory of information can also be confirmed by testing for intrinsic ordering, as an assumption of the method, and therefore the analyses carried out in Study I and Gove et al. (1992, 1995) ought to be replicated for similar studies in the future. It is also worth noting that intrinsic ordering may more easily be accomplished when the number of DBH (or height) classes considered are few, when bin widths are broad (e.g., MacArthur and MacArthur 1961). It is very unclear, however, what the subjective criterion to determine a suitable bin size should be[17]. Moreover, Gastwirth (1972) demonstrated that the use of size classes, by itself, yields to a systematic underestimation of GC, and therefore it is clear that Eqs. (2-3) for $L_r(x_r, M_r)$ should be used instead of Eq. (1) for $P_k(x_k, M_k)$. Many researchers on forest structure characterisation have already argued the disadvantage of subjectivity in bin size determination, and subsequent loss of information (e.g., Kint et al. 2000; Staudhammer and LeMay 2001; Barbeito et al. 2009). Instead, I argue that the problem is that defining entropy between DBH classes is a conceptually wrong way of describing forest structure, and tree DBH inequality ought to be used instead. As DBH (or height) is a continuous variable, it should be described by measurement of dispersion, and not apportioned into bins to describe entropy[18]. If the target of the forest structure characterisation is to compare the situation of maximum entropy, which is worth considering, this can be still evaluated from the reference value given by $GC = 0.5$. Therefore, among all those indicators in Table 1, found in the research literature, I only see a single indicator as valid to describe horizontal differentiation: the Gini coefficient of tree DBH inequality (basal area-weighted).

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[17] Study I's results could actually provide an objective criterion to be determined empirically: bin size must be the smallest that still satisfies intrinsic ordering.

[18] Which does not undermine the fact that the entropy of the DBH distribution should still be studied, if that is the property targeted. Individual trees can still be used to study entropy, instead of DBH classes (see page 49).

3.2 The Lorenz curve of tree size inequality to describe horizontal differentiation in forest structure

3.2.1 The Lorenz curve as a join representation of weighted and unweighted diameter at breast height (DBH) distributions

As explained, the Lorenz ordering is related to majorization (Solomon 1979), as the relative cumulated proportions of basal area ($M_r = \sum_{j=1}^{r} g_j^{\#}/g$) accounted by each tree are represented against relative cumulated proportions of stem density ($x_r = \sum_{j=1}^{r} n_j^{\#}/n = r/n$). Lorenz curves $L_r(x_r, M_r)$ therefore contain information about both the unweighted DBH frequency distribution and the basal area-weighted distribution of a forest. Fig. 3 may illustrate why a full description of forest structure requires characterisations of both the weighted and unweighted DBH distributions. For instance, using a descriptor of the DBH stem frequency distribution alone would not discriminate bimodal (f) from peaked reverse J shapes (e), and therefore unweighted distributions (white bars) are insufficient for diagnosing recruitment in the understory. On the other hand, a reverse J (d) cannot be discriminated from uniform distributions (c), or even mature even/sized forests (b), by a simple descriptor of their basal area-weighted distributions alone (grey bars). Lorenz ordering was therefore considered well-suited for discriminating all kinds of plausible FSTs.

In forest science, the Lorenz curve expresses relationships of relative dominance among individual trees within the forest (Weiner and Thomas 1986). For the concave[19] Lorenz curves considered in this doctoral thesis, the relative dominance of the upper strata is represented in the right tail of the Lorenz curve. On the other hand, the left tail describes the relative rarity of the lower strata, the presence and development of understory and suppressed trees (Study III: Fig. 3). Thus, each portion of the curve is related to the different layers that can be found in a multi-layered forest.

3.2.2 The Gini coefficient

The most straightforward indicator related to Lorenz ordering is the Gini coefficient. The GC is usually conceptualised as the area between the Lorenz curve and the diagonal line-of-absolute-equality, and thus it describes the amplitude of the Lorenz curve. The GC is a quantification of basal area differences between all trees within a plot, normalised by their mean. It is therefore a descriptor of concentration, or relative dispersion.

Values of GC in Fig. 4 show the forest plots in an order which seemed logical according to their structural properties. Table 3 also showed that this has more potential for its estimation by ALS remote sensing that any other indicator of horizontal differentiation. Weiner and Solbrig (1984) were amongst the first to use the GC to study structure in plant ecosystem, using cumulated biomass to apply the method to vascular plants. Knox et al. (1989) concentrated on tree species, finding the GC superior to other indicators based on product moments. Lexerød and Eid (2006) also found GC more beneficial from a practical point of view than using measures of entropy between DBH classes. Using datasets apportioned into size classes may be a burden for GC calculation itself (Gastwirth 1972). Practitioners having input data already arranged by size classes may wish to make use of Duduman's (2011) equation to employ such data types as if they were individual trees,

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[19] From trees ranked according to decreasing DBH

without underestimating GC[20]. Otherwise, I recommend the formula specified in Table 1 whenever a complete tree list is available, applying Glasser's (1962) bias correction $(n/(n-1))$ when estimating it from a sample (Study II: eq. 3).

Study V illustrated the practical application of ALS predictions of GC. Dynamics of forest development regulated by tree mortality, such as canopy disturbance or self-thinning, were revealed by decreases in GC values (Study V: Fig. 4). Seed regeneration and ingrowth increase the structural complexity of the forest, and therefore these processes would be exposed by rises in GC values. Maps similar to those generated during the research work for this doctoral thesis (Study V: Fig. 7; Study VI: Fig. 4) can be used for identifying areas needing silvicultural treatments or evaluating forest recovery after disturbance. The value of ALS remote sensing in assisting forest management is clear (Packalen et al. 2011). GC predictions and FST classifications can provide a useful method directly applicable in management. For instance, more accurate forecasts of forest growth may be achieved by applying separate models for each different FST (de Miguel et al. 2012), or using GC itself as the independent variable (Lei et al. 2009). ALS estimations of GC can also have applications to forest inventory and monitoring. A GC-based stratification into FSTs may assist in increasing the accuracy of carbon budget estimates by reducing the within-strata variability (Asner et al. 2012), which is driven by differences in forest structure between forest areas. Study VI showed that GC predictions can also show divergences at landscape scale between two given forest zones. Forest areas with differing histories of forest management differed in their resulting ALS predictions of GC (Study VI: Fig. 5). Rare events not detected by simple random sampling (Barabesi and Fattorini 1998), such as structural differences at forest stand borderlines or selective logging – legal or illegal – may be more easily identified from wall-to-wall predictions of GC throughout a forest area. Study VI, for instance, discussed the usefulness of the ALS predictions of this indicator to monitor the compliance of management practices with legal restrictions on logging near lakeshores. The third objective (see Section 1.4) of this doctoral thesis was accomplished by illustrating the practicability of this indicator in (1) a static analysis (Study VI) on forest structure status, and also (2) a dynamic analysis (Study V) by comparing plots located in different areas along the full chronosequence of the forest development cycle (c.f. del Río 2003).

3.2.3 The value of representing the theoretical uniform DBH distribution in a Lorenz plot for forest structure diagnosis

Lorenz curves are usually compared to the line-of-absolute-equality, the 1:1 diagonal, obtained when all trees are identical in size. As noted, the GC derives from this concept, creating a scale of dispersion which increases from that line (see page 49). The theoretical values of GC range [0,1] (Gini 1921; Hosking 1990). $GC = 0$ is the value for any forest plot with all trees equal (line-of-absolute-equality), irrespective of their abundance (i.e. density or QMD, sensu Section 1.2). The other extreme of $GC = 1$ would be a maximally bimodal distribution presenting the highest theoretical dispersion. In this doctoral thesis, the

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[20] Note that any cause leading to a loss of precision in DBH measurements of individual trees would yield a similar effect. The event of finding two trees of exactly the same size – which seems very unlikely in the field – could happen if measured by, for example, 1 cm classes, resulting in a DBH difference of zero which would strongly influence the calculation of GC.

importance of comparing Lorenz curves against a theoretical uniform DBH distribution in tree diameters has also been considered (see Study III: Fig. 1). This other line-of-perfect-uniformity has an asymptotic (number of trees $n \to \infty$) theoretical value of $GC = 0.5$. This suggestion was grounded in the rationale used by followed de Camino (1976) and Staudhammer and LeMay (2001). It is not mere chance that the coefficient of homogeneity of de Camino (1976) takes the value $CH = 2$ for this uniform distribution[21], whereas Staudhammer and LeMay's (2001) took the variance of the uniform distribution as the ceiling for their structural index $STVI = 1$. As explained, these values represent the scenario of maximum entropy (Önal 1997b). Study I showed that the diversity and equitability indices could still be used if all the populations compared are either $GC > 0.5$ or $GC < 0.5$, i.e. their variances are all either larger or lower than the uniform distribution's – as was apparently the case for, for example, Buongiorno et al. (1994). Values of GC should also be interpreted according to these theoretical distributions, as GC = 0, 0.5 and 1 for the diagonal, uniform and maximally bimodal, respectively (Study III: Fig. 1). This property is invariant of the species considered and applicable to other forest ecosystems, as is consistent with recent research by Duduman (2011) and Klopcic and Boncina (2011) which also ordered FSTs by increasing GCs as even-sized, uniform, bimodal and reverse J.

3.2.4 Intersecting Lorenz curves and the need for a descriptor of asymmetry: basal area larger than the mean ($BALM$).

Lorenz curves were not totally prone to intersections either (Fig. 7). It was consequently suggested that a full description of forest structure requires the GC to be accompanied by a descriptor of the Lorenz curve's asymmetry or skewness, as Knox et al. (1989) or de Miguel (2012) did with the third moment of the DBH distribution. For this doctoral thesis, I researched the convenience of using an indicator of asymmetry that was tailored to the Lorenz curve by Damgaard and Weiner (2000), reaching interesting relationships with structural stocking properties discussed by Gove (2004): the basal area larger than the mean ($BALM$) and the significance of the QMD with regards to size-biased distribution theory (Gove 2003). Overall, the research conducted during this doctoral thesis leads me to suggest a bivariate description based on GC and $BALM$, as independent indicators of forest structure that, together, accomplish a full description of the Lorenz curve of tree size inequality.

The starting point for describing the skewness of the Lorenz curve was the index of Lorenz asymmetry (LA) proposed by Damgaard and Weiner (2000). They suggested evaluating the shape of the Lorenz curve by means of a description of its inflexion point's position. Study V (eq. 1) includes a formal mathematical demonstration showing that, for the case of a Lorenz curve of tree basal areas, its inflexion point coincides with the QMD. The reason for this lies in the condition that the intersection between a size-biased distribution of second order and its original occurs at the weighted mean (Gove 2003). Consequently, the components of Lorenz asymmetry proposed by Damgaard and Weiner (2000) were, when applied to tree basal areas, in fact, the proportions of basal area $M(x_{QMD})$ and stem density x_{QMD} accounted for by the trees larger than QMD (see footnote #1 on page 9). These have traditionally been applied in forestry, in relation to the use of structural stocking guides (Gove 2004). In particular, the $BALM$ is the value of the y-axis[22] at the position of the Lorenz

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[21] Maximum entropy is $CH = 2$ and maximum dispersion is $CH = 1$, see Fig. 4

[22] This applies to concave Lorenz curves only, which is a good reason to use them in forest science. Convex curves denote the inverse of $BALM$ instead.

curve's inflexion point $M(x_{QMD})$. Correspondingly, we shall also denominate the value of the x-axis (x_{QMD}) as the number of stems larger than the mean ($NSLM$). This doctoral thesis, therefore, provides an original link between the works of Damgaard and Weiner (2000) and Gove (2004). It is also the first time that the concept of $BALM$, which Gove (2004: Fig.1) conceptualised from the relationship between weighted and unweighted DBH density distributions, is also expressed in terms of its significance in the Lorenz curve.

Modification of the original Lorenz asymmetry index was also suggested, to express an average of its components (Study V). The intention was to fix its range within [0,1], and its middle value $LA = 0.5$ for a symmetrical Lorenz curve[23]. This was, however, not entirely accomplished in practice. Although it is true that $LA = 0.5$ would define a symmetric Lorenz curve, the practical dynamic range of LA cannot reach the full [0,1] span of values. The quadratic relationship between DBH and basal area imposes a finite lower limit to the QMD, and therefore to the probability density of the basal area-weighted distributions (Gove and Patil 1998). This effect can be observed in the asymmetry of a theoretical uniform distribution, as the size-biased distribution of second order takes its inflexion point away from the axis of symmetry (dotted line in Study V: Fig. 2)[24]. As a result, the theoretical range of values for $BALM$ and $NSLM$ is in practice much narrower in its lower limit. For instance, Gove (2004) demonstrated that $BALM$ has a maximum range between [0.58, 0.99] for any DBH distribution conforming to a Weibull function. A similar condition affects the $NSLM$, and thereby LA, as some probability density must always be above the QMD. Subsequently, the position of the Lorenz curve's inflexion point cannot reach the entire extent of the Lorenz curve's x,y-axes in practice (Fig. 7). This was signified when the indicators were calculated in Kiihtelysvaara, as the ranges of observed values depicted in the figures of Study IV for LA, $BALM$ and $NSLM$ are narrower than those for GC[25]. Another example can be observed in the application of these indicators by Vihervaara et al. (2014: Fig. 4f and App. 2) in an independent study site, which also showed that the plausible dynamic range for these indicators is constrained in practice.

Results showed that adding LA to the already selected indicator of GC could be beneficial for discriminating between determined FSTs, especially those that are uneven-sized (Fig. 7). When the empirical values of GC and LA were observed together (Fig. 8), the changes in the values of these indicators induced by the dynamics of the shelterwood management system applied in the study area became clear[26]. Setting the uniform FSTs aside[27], the succession in

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[23] Which is a Lorenz curve with its inflexion point at the axis of symmetry, see Damgaard and Weiner (2000: Fig. 1)

[24] Its skewness would be higher if employing volume or biomass, i.e. a third order size-biased distribution (Gove 2003)

[25] And therefore their relative RMSEs are not directly comparable. It should not be concluded from results in Study IV that some indicators are more reliably estimated by ALS than others.

[26] In addition to the differences among FSTs, the tilt of ellipses of confidence also provides an idea of the directions of change in these indicators motivated by forest development.

[27] Uniform DBH distributions were regarded as simply representing a boundary state, as plots were quite big (20-m radii) and they could be located close to the drip-line of a canopy gap, containing trees from two different FSTs (Study I). This begs the question of which scale is to be used for determining these indicators (see Section 3.4.2).

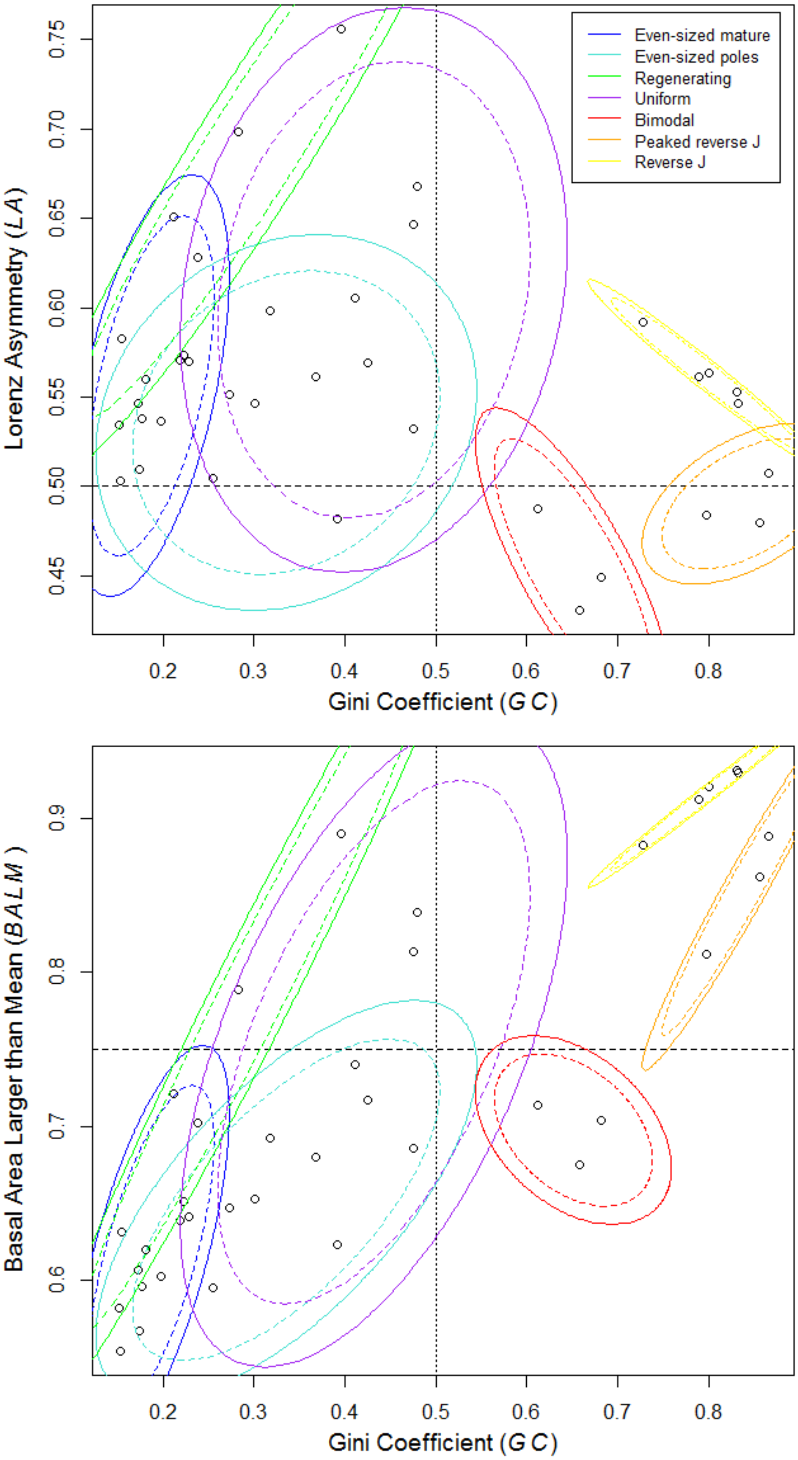

Figure 7. Scatterplots of Gini Coefficient against Lorenz asymmetry (upper) and Basal area Larger than Mean (lower), calculated from plot-level field data. Confidence ellipses at 95% (dashed lines) and 99% (solid) for each forest structural type constructed from a χ^2 distribution.

forest development completed a cycle around this bivariate description (these processes are summarised in Figs. 3-4 of Study V). Values of $LA > 0.5$ showed that seed regeneration occurring in canopy gaps after forest disturbance induced a sudden skew of the Lorenz curve (from mature to regeneration, see also the green curves in Fig.7). After that, the development of natural regeneration yielded a relatively quick increase in GC, which continued until forest structure balanced into reverse J. These were stages of shade-intolerant regeneration after disturbance, with no resource limitation, until reaching stem exclusion stage (Coomes and Allen 2007). If recruitment occurs under the dominant canopy, such as by shade-tolerant regeneration, the Lorenz curve becomes more symmetric, turning toward $LA < 0.5$ if a subdominant cohort establishes under the dominant canopy. Mortality patterns involving higher death rates for larger trees (Coomes et al. 2003), again result in Lorenz asymmetry turning back to $LA > 0.5$. Shelf-thinning processes driven by asymmetric competition (Weiner and Thomas 1986), on the other hand, do not induce major changes in Lorenz curve skewness. Both processes, nevertheless, are signified by a steady decrease in GC as a forest develops toward maturity, closing the cycle.

The results of the PLS analysis carried out in Study II (Fig. 2) reflected the inverse relationship between $BALM$ and $NSLM$, which makes them cancel each other out in their averaged indicator LA. Consequently, although Study V suggested a bivariate description of forests based on GC and LA, I further suggest that the latter shall be simply substituted by $BALM$, as the components of Lorenz asymmetry are interdependent – since $M_{QMD}(x_{QMD})$, viz. $BALM(NSLM)$ –. $BALM$ is easier to conceptualise and quicker to diagnose from an empirical concave Lorenz curve, as the y-axis position of its inflexion point.

When the distribution of FST was observed over the bivariate $(GC, BALM)$ description (lower scatterplot in Fig. 8), the results complied with the conclusions reached for LA, and yet $BALM$ added few more interesting features to the analysis. Shade-intolerant regeneration with resource depletion, but not resource pre-emption (Weiner 1985), was signified by high values of $BALM$. Again, these occur in the period from canopy disturbance and development until the stem exclusion stage. Competitive thinning and mature thinning (Coomes and Allen 2007) are both signified by this, by the above-mention decrease in GC, which is therefore closely inter-related to asymmetric competition (Cordonnier and Kunstler 2014). Most importantly, these stages of either shade-tolerant regeneration or shelf-thinning (in the case shade-intolerant species) are both characterised by occurring at low $BALM$ values. Thus, there is a threshold separating symmetric competition – which allows for shade-intolerant regeneration – from asymmetric competition – which leads to mortality, and only allows for shade-tolerant regeneration (Schwinning and Weiner 1998) – which is clearly marked by $BALM$. This threshold seems to be approximately at the middle value of its practical dynamic range, at approximately $BALM = 0.75$. Although further research should be aimed at determining the exact value of $BALM$ that would define a frontier between symmetric and asymmetric competition, this approximate value has been depicted in Fig. 8 to show the clear distribution of FSTs in the $(GC, BALM)$ scatterplot. For clarity, all these processes have been summarised in Table 4.

Table 4. Summary of processes that can be seen with the suggested indicators.

	Gini Coefficient	Lorenz Asymmetry	Basal Area Larger than Mean
Increase	Tree growth	Mortality in dominant canopy	Symmetric competition (resource depletion)
Decrease	Tree mortality	Ingrowth in understory	Asymmetric competition (resource pre-emption)

At this point, it is worth describing how $BALM$ relates to BAL_i, with the intention of stressing its value in modelling tree competition, and in general the asymmetry of a population's distribution. BAL_i is the basal area accumulated by the trees larger than a given tree i (Wykoff 1990; Vanclay 1994), which therefore has a competitive advantage by playing a role in resource pre-emption (Thomas and Weiner 1989). BAL_i is employed as a descriptor for size asymmetric competition for individual trees (Coomes et al. 2011). Cordonnier and Kunstler (2014) have recently identified its relationship to the GC. BAL_i works at the individual tree level, however. At population level, $BALM$ is the share of the basal area larger than a tree whose diameter would equal the QMD ($BAL_{DBH_i=QMD}$). $BALM$ should therefore be employed to define the level of asymmetric competition in uneven-sized stands (cf. Study V: Fig.5) from very asymmetric (reverse J) to lesser asymmetry (bimodal). It can be used as a stand level parameter similar to BAL_i, but describing the overall competition conditions among trees in a forest grove.

3.2.5 In a nutshell: the major findings of this doctoral thesis regarding Lorenz ordering of tree size inequality

A Lorenz curve of tree size inequality represents the relationships of relative dominance among trees in a forest population. It is calculated by comparing the cumulative share that each tree has to the total stem density against the cumulative share to the total basal area (Solomon and Gove 1999), although some authors have also employed volume (de Camino 1976) or biomass (Weiner and Thomas 1986). Results in this doctoral thesis have shown mathematical advantages gained from the use of tree basal areas, as the quadratic relationship between the diameter of each tree and its basal area (Gove 2003) tightly determines the asymmetry of the Lorenz curves. The GC of tree basal area inequality is the indicator of horizontal differentiation chosen among those in Table 1. We considered the convenience of comparing empirical Lorenz curves against a theoretical uniform DBH frequency distribution (shown in Study 1, Fig. 4), which may be analytically determined by its asymptotic value at $GC = 0.5$. It was also demonstrated in this doctoral thesis that the inflexion point of the Lorenz curve coincides with the QMD (Study V: Eq. 1), a property which has general usefulness in forestry (Curtis and Marshall 2000). This also led to the idea of employing $BALM$ (Gove 2004) as a descriptor of the Lorenz curve asymmetry. $BALM$ was demonstrated to be one of the components of Lorenz asymmetry (denominated M_{QMD} following the notation of Damgaard and Weiner (2000)). The final recommendation is a bivariate description of forest structure by GC and $BALM$, which provides a full description of horizontal differentiation properties between stems in the forest.

3.3 Predicting the chosen Lorenz structural indicators with ALS remote sensing.

Once the most suitable forest response to target was clarified, which was the main objective of this research, the following tasks aimed at generating prediction maps of these indicators in the study areas and provide them with practical applications in forest inventory and management planning. This doctoral thesis has not developed many significant advances in ALS remote sensing or estimation methods, but rather focused on implementing the current state-of-the-art methods for the described indicators. This state-of-the-art in ALS estimation was revised in quite an exhaustive manner (Fig. 2, Study IV: Fig.1). For this reason, results for prediction are not meticulously summarised, and only the major findings are highlighted below. The articles themselves give more detail of the findings, opportunities and difficulties further encountered, and therefore they are to be read along with the body of this thesis.

Generally speaking, area-based methods for ALS involved extracting the returns over a given area and generating a large array of statistics from the distributions of their heights above the ground. These are called ALS metrics, and they are used as predictor variables for the target response, using a variety of estimation techniques. These metrics are strongly correlated to one another, and a method for predictor selection is thus required (this is perhaps one of the most challenging tasks, and about which there is less consensus). Throughout the thesis, and across studies, these ALS metrics are referred to using acronyms (Tables 3 and 5), whose explanation can be found in the appendix. The reader unspecialised in ALS remote sensing may refer to the user manual of the software used (McGaughey 2012), or the more general explanations of ALS prediction in Maltamo et al. (2014), although Study IV can also be read as a review article including specific operational details. The array of methodologies summarised in Fig. 2 shall be expanded by the different estimation strategies explained in Study IV: Fig 1. To my knowledge, this comparison was a complete revision of the complete span of possibilities in ALS estimation. There is, perhaps only one alternative strategy on estimation which is lacking, and that would be to consider parameters for theoretical functions fitting weighted and unweighted DBH distributions to be used as a response[28] (Gobakken and Næsset 2004; Maltamo et al. 2007). ITD methods were not exhaustively reviewed, only considering those included in Packalen et al. (2013) and Vauhkonen et al. (2014). So many methods were employed in order to explore the benefits and possibilities of each during the research work. Their common assessment also allows identification of which results remain invariant across methods, and discriminates those which are obtained by mere chance. These are the results emphasised in the subsections below.

3.3.1 Relationship of ALS remote sensing with the Lorenz curve unveiled

The CCA carried out in Study III showed that most of the potential of ALS remote sensing for explaining variability in the Lorenz curve of tree size inequality came from metrics related to the concentration (relative dispersion) of ALS return heights. One such metric was the L-coefficient of variation of return heights ($L.CV$). This is not mere chance, as the L-coefficient of variation is equivalent to the Gini coefficient (Hosking 1990). This is highly relevant as it demonstrates that the Lorenz curves from tree sizes and return heights are closely related. This equivalence reveals that the properties observed for GC in relation to describing empirical DBH distributions must stand for the distributions of laser height as well. The study of separate canonical components also allowed us to observe the correlation of certain metrics with each segment of the curve (Study III: Fig. 3), detailing the effects that can be observed in ALS surveys in relation to tree stocking balance relationships in multi-layered forests. The first CCA component was more related to the dominant canopy, and therefore it influences the ALS surveys to a greater extent. This dominant layer is mainly described by canopy cover metrics, and thus it depends mainly on the forest stand's relative density. The second CCA component was more related to the development of the understory, which influences the total number of returns observed and the skewness of their heights. During the predictive modelling carried out in Studies II, IV, V and VI, some degree of recurrence in certain metrics across methods and study areas was also noted (Section 3.3.2). This further reveals the potential for future development of trans-national indicators of forest structure related to the Lorenz curve of tree size inequality. We therefore encourage research effort clarifying whether such relationships can also be found across bio-geographic regions.

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[28] Which would be an approach between Strategies B and C in Study IV: Fig. 1.

The results obtained in the CCA analysis showed the advantage of considering discrete portions along the Lorenz curve (Study III: Table 2). They allowed us to attain a more profound understanding of the effects that ALS metrics have at different segments of the curve. It can be seen that each canonical component was roughly focused on either half of the curve. This is denoted by larger absolute coefficient values obtained for either tail of the curve at each CCA component. The $M(.05-.25)$ quantiles obtained higher values in the first CCA component, and thus, the predictors showing higher coefficient values in this component are more related to the upper strata. On the other hand, the $M(.55-.95)$ quantiles were mainly represented in the second CCA, and its corresponding ALS metrics are thus more related to the degree of development in the lower strata. The middle part of the Lorenz curve, in the region of $M(.20-.50)$, is the area that distances itself the most from the diagonal. It is therefore the segment most closely related to the GC of DBH inequality.

The Lorenz curve expresses relationships of relative dominance between forest vertical strata which are revealed by the characteristics of lidar pulse interception by the canopy. As tree dominance in a forest is driven by competition for light, similar relationships must also apply to the backscattering properties of a laser footprint which reaches that canopy from above. The study of the Lorenz curve is, for this reason, a reliable method for analysing forest structural characteristics related to tree size inequality. Lorenz ordering expresses the dominance between overstory and understory in relative terms (Study III: Fig. 3), just like the different portions of a laser footprint which return to the sensor. This presents an opportunity to deduce physical relationships between laser pulse echoes and canopy components. The Lorenz curve therefore offers the potential to develop unsupervised methods for lidar sensors reaching the canopy in a nadir direction.

While Study III considered the relationships of ALS metrics along the full Lorenz curve, Study II concentrated on the chosen indicators themselves. The resulting MMI models showed GC and $BALM$ to be explained by essentially different sets of ALS metrics (Study II: Table 3). This was not exactly the case for $NSLM$. Regarding LA, as their components expressed opposing cause-effect relationships (Study II: Fig. 2)., the overall indicators showed little variation explained by the ALS metrics (Study II: Table 2). As a consequence, few of the methods used for LA estimation achieved reliable results (Study IV). It can also be confirmed that among all the comparisons carried out in Study IV, the results for $BALM$ were in most cases better than those for $NSLM$. These are just additional arguments in favour of recommending this bivariate description of forest structure by ALS.

3.3.2 Recurrence of ALS predictor selection results across methods and study areas

The results obtained across Studies II-VI demonstrated that certain ALS metrics were closely related to the target indicators. Although a great variety of ALS methods for estimation and predictor selection have been covered in this doctoral thesis (Fig. 2 and Study IV: Fig. 1), many predictors have been reclusively selected in the predictive modelling. Table 5 is a compilation of all the results obtained in these studies, highlighting the most recursive metrics.

Indices of concentration, dispersion of return heights relative to their average, demonstrated high explanatory potential for both GC and $BALM$. Such types of ALS metrics were the coefficient of variation (*CV*) and *L.CV* – which are ratios of second and first moments – or the median absolute deviation from the median (*MAD.median*). There are also some similar ones, simply expressing the spread of ALS returns, such as standard (*SD*) or average absolute deviation (*AAD*).

Table 5. Summary of variable selection results obtained for all the articles, study areas, and methods employed for this doctoral thesis. See full description of ALS metrics in appendix.

Indicator	Study area	Variable selection / Modelling method	ALS metrics	Study
Gini coefficient	Valsaín	Correlation	*SD; P10; L2;* ***L.CV***	II
		best subset AIC / LM	***Max****; SD; P10, P25;* ***Cover.mean***	II
		MMI / beta regression	***Max****; SD; P25;* ***Cover***	II; V
	Kiihtelysvaara	best subset AIC / LM	*P05;* ***L.CV****;* ***Cover****;* ***Cover.mode****; Cover.f.mode*	IV
		best subset RMSE / LM	***P95****;* ***L.CV****;* ***Cover***	VI
		LASSO	*Mode; Skew;* ***P99****;* ***Cover****;* ***Cover.mean****; Cover.f; Count/f*	IV
		RF	***Max****; P20; L.Kurt;* ***Cover****; Count/f*	IV
		MSN (CCA)	***L.CV****;* ***Cover****; Cover.f; Count; Count.f*	IV
	Koli	best subset RMSE / LM	***L.CV****;* ***Cover****;* ***Cover.mode****;*	VI
Lorenz asymmetry	Valsaín	Correlation	***Cover***	II
		best subset AIC / LM	*L.skew;* ***Cover.mean***	II
		MMI / beta regression	*L.slew;* ***Cover***	II; V
	Kiihtelysvaara	best subset AIC / LM	*MAD.median; Cover.mode/f*	IV
		LASSO	*Mode; CV; Kurt; MAD.median; P01; P40; L4;* ***Cover****; Cover.f.mode; Count/f*	IV
		RF	*CV; Kurt; P40; L4*	IV
		MSN (CCA)	*MAD.median; P01; P40; L4*	IV
BALM	Valsaín	Correlation	***SD****;* ***CV****; IQR; L2;* ***L.CV***	II
		PLS	***SD****; P90; L2*	II
		best subset AIC/ LM	***SD****;* ***AAD****; L.Kurt;* ***Cover.mean***	II
	Kiihtelysvaara	best subset AIC / LM	***MAD.median****; Skew;* ***Cover****; Cover.f.mode*	IV
		LASSO	*Mode; Skew; Kurt;* ***MAD.median****; P10; P20; P30; L4;* ***Cover****; Cover.mean; Cover.f.mode; Count/f*	IV
		RF	*Skew; Kurt;* ***MAD.median****; P30; L4*	IV
		MSN (CCA)	*Skew;* ***MAD.median****; L4; Cover; Cover.mean; Cover.f.mode*	IV
NSLM	Valsaín	Correlation	*CV;* ***Kurt****; P10; L2; L.CV*	II
		PLS	*P25;* ***L.Kurt****;* ***Cover***	II
		best subset AIC/ LM	*SD; P10, P90; L2;* ***Cover.mean***	II
	Kiihtelysvaara	best subset AIC / LM	*P70;* ***Cover****; Cover.mode; Cover.mean/f; Cover.mode/f*	IV
		LASSO	***Kurt****; Count/f*	IV
		RF	*P20; P25;* ***L.Kurt****;* ***Cover***	IV
		MSN (CCA)	*Mode; P60; P70; L.CV;* ***Cover****; Cover.f; Cover.f.mean*	IV
Lorenz curve	Kiihtelysvaara	CCA	*CV;* ***L.CV****; Count.f;* ***Cover.mode***	III

AAD: average absolute deviation of ALS heights.
MAD.median: median abs. dev. of ALS heights.
L2: second L-moment of ALS heights.
L.CV: L-coefficient of variation of ALS heights.
L.Kurt: 4th L-moment ratio of ALS heights.

P.95 - P90: 95th and 90th percentile of ALS heights.
Cover.mean: proportion of ALS heights above mean
Cover.mode: proportion of ALS heights above mode
More metrics described in Table 3; Table A1, Study IV; Table 1, Studies II-III and V; and McGaughey (2012)

Another important lesson learned from the overall analysis shown in Table 5 was that canopy cover metrics played an important role across metrics. Such type of metrics evaluate proportions of ALS returns backscattered below certain height thresholds. These are the proportion of return heights above their mean (*Cover.mean*) mode (*Cover.mode*) and above 1 m (*Cover*). This signifies the relationship between forest structure and canopy cover properties, probably in relation to the above-mentioned properties of symmetric and asymmetric competition. Such relationships would need to be further clarified by future research.

3.3.3 Choice of method: preference of area-based methods over individual tree detection

The results of Study IV were statistically sound for all the methods following area-based approaches: i.e. ALS returns are extracted for a given area and statistical metrics computed from them and used as auxiliary variables for the prediction. Most approaches obtained comparable accuracies (Study IV: Tables 1-3). The choice of method may therefore depend more on the properties of the final outcome, such as the distribution of the residual variance. When MSN imputation was used to compute an entire diameter distribution, the accuracy of the resulting indicators was greater than when estimating the Lorenz curve or approaching direct indicators estimation. Tree list estimation may therefore be of interest in studies focused on the structural properties of forests. The Lorenz curve estimation may be advantageous if interested in a deeper exploration of the relationships of dominance between canopy strata (Study III), but not for predicting the target indicators.

Approaches based on individual tree detection tend to omit suppressed trees, and therefore underestimate the understory. Our results suggest that they may be clearly inferior to area-based approaches with regards to describing the structural properties related to tree size inequality in forested areas, and Packalen et al. (2013) faced similar problems in predicting spatial patterns. Although the semi-ITD approach may correct the biasing underestimation of tree size inequality obtained by ITD, any approach involving CHM segmentation was demonstrably inferior to plot level training, with regards to estimating forest structure indicators based on the Lorenz curve. As ITD methods have not been exhaustively reviewed, however, these result do not prevent more sophisticated ITD approaches from being beneficial for predicting forest structure indicators.

3.4 Future research towards pan-European implementation

3.4.1 At what scale should forest structure be assessed and estimated?

An important question that remains unanswered is the scale at which the ALS indicators have to be assessed. During Study V a scale-dependent bias was noted which was inherent to the method, since when enlarging the size of a forest plot, the probability of finding a tree of different size is higher, and therefore the GC increases (as does any similar indicator, see Zenner et al. (2005)). This is an intrinsic drawback of using an area-based method, and thus future research should aim to determine the optimal scale for assessing forest structure indicators. The effect of scale on the Lorenz indicators considered was one important issue, as detailed in Study V. In the case of Study VI, since the study was carried out using plots differing in size, there could be a potentially small influence of the scale on the results. However, since plot size was determined according to stand density, the number of trees included in each can be considered roughly similar. Therefore, even though the field plots used for these estimations differ in plot area, they are equal in terms of sample size. The scale used also affects different ALS metrics in another way, and it is not clear whether these effects are synergetic for the Lorenz indicators and the ALS metrics, affecting the estimation itself. Whether these indicators are more affected by the scale or the sample size, or this effect is also affecting the ALS estimation of Lorenz indicators, are questions to be clarified in future research.

3.4.2 Developing pan-European indicators of forest structure by means of ALS remote sensing.

The research conducted in this thesis indicates the Lorenz curve as a promising approach in the field of ALS remote sensing. The methods have, however, only been tested in managed conifer monocultures, and can therefore still be little generalised. Further research should take the necessary steps to link the Lorenz-based indicators with a boarded list of FST classes covering all kinds of European forest ecosystems. In order to accomplish that, the ecological functions of ALS-derived FSTs ought to be studied at different biogeographical regions. Competition for resources defines differing factors determining forest growth and decline in diverse areas of Europe. The effect of this variability has not yet been studied, and requires research into populations comprised of both shade-tolerant and shade-intolerant species. These indicators could then be employed in ALS to assist in establishing whether limiting factors determining growth and mortality are competition for light or water for a given ecosystem (Jucker et al. 2014).

3.4.3 Timeliness and opportunity: the advent of national ALS surveying programmes (NASPs)

ALS reaches the ground underneath vegetation, giving unprecedented topographic information (Baltsavias 1999). For this reason, many countries in Europe – and the world – have invested in nationwide ALS survey programmes (NASPs) in recent years, primarily to obtain high-resolution DTMs (i.e. terrain contour maps). There is a critical trade-off between the cost of surveying and laser pulse density, which determines the spatial resolution of the ALS product. DTM production can be carried out at low densities (less than 1 pulse per squared-metre), which enables the ALS surveillance of entire countries. Although forest applications usually rely on higher densities, the use of a national ALS dataset at no extra cost may still be beneficial (Villikka et al. 2012; González-Ferreiro et al. 2014). Although the point density of these datasets is relatively low, they are also demonstrably useful for forestry and ecological applications (Vihervaara et al. 2014). There should be further study of whether similar conclusions may still be drawn from these datasets, or if higher densities would be required for reliably determining these indicators or reaching the full span of plausible FSTs.

National ALS surveying programmes (NASPs) are currently ongoing throughout Europe. Examples are: Finland (NLSF 2015), United Kingdom (ARSF 2015), Spain (PNOA 2015), Denmark (Kortforsyningen 2015), and Netherlands (AHN2 2015), as well as others in Germany, France, Sweden, Italy, Norway, Austria, Switzerland, etc. Many of these NASP datasets are openly available, and more will become public under EU agreements to make environmental information accessible. The multiplicity of ALS systems and flight parameters have obstructed the development of consistent and invariant methodologies in the past (Næsset 2009), however there is now a general consensus of the optimal parameters for laser surveying, and all NASPs are carrying out using similar procedures (Ahokas et al. 2005). Thus, the current situation poses a unique opportunity for:

- Generating forest indicators and classifications that can be consistently obtained throughout entire countries in Europe, with the ultimate goal of deriving them at a pan-European level.
- Developing methods that can be directly replicated by any interested party or stakeholder, given the public nature of these laser datasets and the availability of open-source tools, which supports the potential implementation of pan-European indicators from ALS in practice.

The scenario is therefore set to allow the implementation of a remote sensing-based pan-European forest structure indicator scheme in practice, in the near future.

4 CONCLUSIONS

Concrete conclusions about the objectives of this doctoral thesis can be outlined from the presented research.

(1) What are the most suitable indicators that can be obtained from the forest data itself?

- The link between intrinsic diversity and Lorenz ordering was established, arguing for disregarding the use of the theory of information and generalised entropy for the purpose of describing horizontal differentiation.
- Even-sized stands are intrinsically non-comparable to uneven-sized stands with regard to the diversity of DBH classes. Indices describing the diversity of size classes are consequently inadequate, as they order FSTs inconsistently.
- Descriptors of the Lorenz curve, such as the Gini coefficient (GC), have been found to be the most reliable indicators for studying forest structure, outperforming alternatives such as variance or diversity indices.
- A particular interpretation of Lorenz curves applies when they are used for the study of forest structures, as they should also be compared to a theoretical uniform distribution, which represents maximum entropy. The Lorenz curve is a method that allows the evaluation of dispersion and entropy simultaneously. The middle value at $GC = 0.5$ represents maximum entropy, and the highest value at $GC = 1$ represents maximum dispersion.
- A descriptor of asymmetry should be used to accompany GC. The basal area larger than the mean ($BALM$) was suggested for this purpose, which is the value of the y-axis at a concave Lorenz curve inflexion point.

(2) Which of those indicators can be reliably estimated from ALS remote sensing?

- The GC of tree DBH inequality is highly correlated with some specific ALS metrics, which are mainly descriptors of concentration in the distribution ALS heights, and also ALS metrics expressing canopy coverage.
- Some indicators, which are valid from a forest science viewpoint, show lower correlation with ALS metrics than those chosen: unweighted equitability indices, de Camino’s homogeneity, and the structural index based on variance (STVI).
- ALS metrics explain variance in opposing directions for each of the components of Lorenz asymmetry, and therefore the skewness of the Lorenz curve can simply be expressed by $BALM$.

(3) What is the best estimation method for obtaining those indicators?

- An area-based method with estimation carried out by MSN imputation of tree lists was among the approaches obtaining reliable accuracies. This method also has many additional advantages, such as better distributing the residual variance along the predictive range.
- Approaches based on individual tree detection are clearly inferior to area-based approaches with regards to describing the structural properties related to tree size inequality in forested areas, due to the underestimation of understory, and they are therefore discouraged for the analysis of forest structure.

(4) Are the ALS predictions of the selected indicators useful for forest inventory, monitoring and management?

- Lorenz curve descriptors of tree diameter inequality were useful for characterising the dynamics of forest development along the shelterwood management cycle.
- Tree mortality decreases GC, whereas tree growth increases GC.
- The asymmetry of the Lorenz curve can be studied to describe the balance between overstory and understory.
- High $BALM$ allows for symmetric competition, whereas asymmetric competition is signified by low $BALM$ values.
- ALS predictions of these indicators can be used in forest management for identifying areas needing silvicultural treatments or evaluating forest recovery from disturbances.
- ALS predictions of GC may be used to monitor the effects of management practice, as well as verifying its compliance with law restrictions.

The final recommendations for pan-European indicators of forest structural complexity based on horizontal differentiation are: GC (describing concentration - homogeneity), and $BALM$ (describing asymmetry - dominance).

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APPENDIX: LIST OF ALS METRICS

Statistics computed from the distribution of ALS return heights (McGaughey 2012):

Min	Minimum
Max	Maximum
Mean	Mean
P50	Median (i.e. 50th percentile)
Mode	Mode
SD	Standard deviation
CV	Coefficient of variation
Skew	Skewness
Kurt	Kurtosis
AAD	Average absolute deviation
MAD.Median	Median of the absolute deviations from the overall median
MAD.Mode	Median of the absolute deviations from the overall mode
L1, L2, L3, L4	L-moments
L.CV	L-coefficient of variation
L.Skew	L-moment skewness
L.Kurt	L-moment kurtosis
P10, P20... …P80, P90	Percentile values (1st, 5th, 10th , 20th, 25th, 30th, 40th, 50th, 60th, 70th, 75th, 80th, 90th, 95th, 99th percentiles)
Count	Number of returns
Count.f	Number of first returns
Cover	Percentage of all returns above one metre
Cover.mean	Percentage of all returns above the mean height
Cover.mode	Percentage of all returns above the mode height
Cover.f	Percentage of first returns above one metre
Cover.f.mean	Percentage of first returns above the mean height
Cover.f.mode	Percentage of first returns above the mode height
Count/f	Number of returns above one metre / total first returns * 100
Cover.mean/f	Number of returns above the mean height / total first returns * 100
Cover.mode/f	Number of returns above the mode height / total first returns * 100