Influence of harvesting intensity on species and structural diversity of forests

Thesis submitted in partial fulfilment of the
requirements of the degree *Doctor rer. nat.* of the
Faculty of Environmental and Natural Resources,
Albert-Ludwigs-Universität,
Freiburg im Breisgau, Germany

by

Felix Storch

Freiburg im Breisgau, Germany

2018

Dean: Prof. Dr. Tim Freytag

First examiner: Prof. Dr. Jürgen Bauhus

Second examiner: Prof. Dr. Andreas Bolte

Third examiner: Prof. Dr. Carsten F. Dormann

Date of thesis defence: 08th of November 2018

Statement of Originality

I hereby declare that this thesis was never been submitted to any other examination committee in Germany or in any other country in order to obtain the same or a similar degree. To my knowledge, this thesis does not contain any material previously published or written by any other person except where proper acknowledgement is made.

Felix Storch

Freiburg, July 2018

Acknowledgements

First of all, I want to thank Dr. Gerald Kändler who gave me the opportunity to work in the field of forest inventories in the Forest Research Institute of Baden-Württemberg (Department of Biometry, FVA BW). Growing interest in the National Forest Inventory and its analyses led to a research position in the department of Forest Conservation. There, in the team of Dr. Veronika Braunisch (Department of Forest Reserve Research, FVA BW), the link towards species diversity and inventories of forest reserves was performed and by that, interest for this PhD-project grew. Additionally, Dr. Kändler was advisor in this project and always very supportive in his recommendations, especially at inventory questions.

I am further grateful to my supervisor Prof. Dr. Jürgen Bauhus (Chair of Silviculture, University of Freiburg), who gave me the option to work in this project, as well as for his patience and inputs regarding this study, which made it an interesting time. The ideas and contributions were very gainful and his support in writing will not be forgotten.

Prof. Dr. Carsten F. Dormann (Chair of Biometry, University of Freiburg) – co-supervisor of this thesis- was very supporting in statistical analysis and therefore special thanks for his inputs. His connections to the German Biodiversity Exploratories were helpful, especially for the request of different data sets.

Thanks to Prof. Dr. Anreas Bolte (Thünen Institute of Forest Ecosystems, Eberswalde) for the willingness to be co-referent of my thesis.

I am also very grateful for the support of my parents, Johann and Claudia Storch, during this project and all my life, as well as all my friends and colleagues, encouraging me in this project.

Special thanks to Joachim Maack for his support in statistical analysis in R.

I want to thank Dr. David Forrester (Department of Forest Resources und Forest Management, WSL Birmensdorf, Switzerland) for his support in proof-reading of parts of the thesis (general introduction and synthesis).

Klaus Winkler (Department of Forest Conservation, FVA BW) was very cooperative regarding information about individual tree species and their types of bark over different developmental stages, which was necessary to calculate the index-variable ‘Bark-diversity’ and therefore huge thanks.

I want to thank the team of the German Biodiversity Exploratories – especially the owners of the applied data-sets – for their input and support regarding my analysis. This was an important part of my study and the link towards species diversity would not have been possible without them. Information about the German Biodiversity Exploratories can be found at http://www.biodiversity-exploratories.de/1/home/

Prof. Dr. Jörg Müller (University of Würzburg) and Torben Hilmers (University of Munich) were very friendly and cooperative with additional data on taxonomic groups of the Bavarian National Park, which were finally not applied in this analysis, caused by a lack of time and further data based difficulties.

During my 2 week stay at the Thünen-Institute of Forest Ecosystems, Eberswalde, I got in-depth insights in organisation and implementation of the National Forest Inventory of Germany. There, especially Dr. Heino Polley and Franz Kroiher were very friendly during my stay and explained everything with patience and enthusiasm to me which made the visit a great experience. The upcoming accommodation of the calculated index values to the National Forest Inventory database (https://bwi.info/) and its assessments is a great achievement and underlines the importance of this study.

Last but not least I want to thank the Team of *BBW-ForWerts* graduate programme in Heidelberg, supervised by Prof. Dr. Thomas Rausch and the team of Dr. Ines Petersen, Anni Mandel, Jean Maples and Hanni Truong who were very supportive in all kind of thinks and gave this graduate school always a friendly atmosphere – especially the summer schools in 2015 and 2016 were organised and prepared in a great way and the financial support for traveling and overnight stays was unproblematic. The networking to other research fields was a great experience, which would not have been possible in this way without the graduate programme. Further information about *BBW-ForWerts*, the fields of research, as well as the participants and their projects can be found at https://biooekonomie-bw.uni-hohenheim.de.

This research was founded by the Ministry of Science, Research and the Arts Baden-Württemberg (7533-10-5-78).

Table of contents

List of Figures X

List of Tables XI

List of Abbreviations XII

Publications and Contributions of Co-authors XIII

Summary XIV

Zusammenfassung XVII

1. General Introduction 1

1.1 The role of forests in the bioeconomy 1

1.2 Importance of structural diversity in forests 4

1.3 Structure and research questions of this thesis 7

1.4 References 12

Chapter 2: Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring 18

2.1 Abstract 20

2.2 Introduction 21

2.2.1 The importance of forest structural elements for biodiversity monitoring 21

2.2.2 Existing indices on structural diversity of forests 22

2.2.3 Large-scale inventories to support biodiversity monitoring 23

2.2.4 Study aims 25

2.3 Material and Methods 25

2.3.1 The study area 28

2.4 Results and Discussion 28

2.4.1 Aspects of structural diversity 28

2.4.2 Core variables of structural attributes 29

2.4.3 Scaling of variables to derive index values 31

2.4.4 Scaling up from plot to forest type-level 31

2.4.5 Assessment of absolute FSI-scores 36

2.4.6 Angle count sampling and transfer to different inventory methods 37

2.5 Conclusion 39

Acknowledgements 39

2.6 References 40

Chapter 3: Linking structural- to species-diversity of forests: An index-based approach 51

3.1 Abstract 53

3.2 Introduction 54
3.3 Material & Methods 56
3.3.1 Study sites 56
3.3.2 Structural diversity index (FSI) 57
3.3.3 Data preparation of different taxonomic groups 59
3.3.4 Data analysis in R 59
3.4. Results 60
3.4.1Variation in forest structural diversity 60
3.4.2 Relationships between structural diversity and species richness of different taxonomic groups 61
3.5 Discussion 66
3.5.1 Performance of the FSI 66
3.5.2 Relationships between forest structure and species richness 67
3.6 Conclusion 69
Acknowledgements 70
3.7 References 71
Chapter 4: Assessing the influence of harvesting intensities on structural diversity of forests in SW-Germany 75
4.1 Abstract 77
4.2 Introduction 78
4.3 Material & Methods 80
4.3.1 Data basis 80
4.3.2 Structural diversity index (FSI) 80
4.3.3 Calculation of harvesting intensities and relation to changes in structural diversity 81
4.4 Results 83
4.5 Discussion 87
4.5.1 Assessment of the NFI for questions on structural diversity and its development 87
4.5.2 Assessment of harvesting intensities for period NFI_{2002} – NFI_{2012} in different types of forests 90
4.5.3 Recommendations for future harvesting intensities in different forest types 91
4.6 Conclusion 93
Acknowledgements 93
4.7 References 94
5. Synthesis 99
5.1 Assessment of the NFI for questions on structural diversity 99

5.1.1 Inventory design 100

5.1.2 Harvesting intensity and limitations of the NFI and alternative data sets 102

5.2 Assessment and application of the FSI 105

5.3 The relationship between FSI and taxonomic groups 107

5.4 Recommendations for future research 108

5.5 References 110

Chapter 2 supporting information I Sampling design of NFI in Germany; Elements and methods of data sampling applied in NFI_{2002} and NFI_{2012} of Germany 113

Chapter 2 supporting information II Transformation of variables into scores (between 0 and 1) based on variable-values of NFI_{2002} and literature 114

Chapter 2 supporting information III Comprehensive list of variables derived from NFI_{2002} and NFI_{2012} 115

Chapter 2 supporting information IV Variables, aspects of structural diversity and correlations with other calculated variables of the comprehensive list of structural attributes 119

Chapter 2 supporting information V Analysed forest types and corresponding number of sampled plots, distributed over Baden-Württemberg, Germany 120

Chapter 2 supporting information VI FSI-distribution for a selection of different forest types of Baden-Württemberg for NFI_{2002} and NFI_{2012} 121

Chapter 2 supporting information VII Overview of analysed forest types and FSI-scores for NFI_{2002} and NFI_{2012} 123

Chapter 3 supporting information I Aspects and associated variables of structural diversity, included in the FSI (taken from chapter 2). Example calculation on plot level 124

Chapter 3 supporting information II: see chapter 2 supporting information III 124

Chapter 3 supporting information III Histograms for different types of forests or regions of the German Biodiversity Exploratories 125

Chapter 3 supporting information IV Mean Index-scores for analysed types of forests of the GBE and equivalent forests types in the NFI-data 126

Chapter 3 supporting information V Overview of the analysis, selection of taxonomic groups and correlation coefficient of the calculated FSI 127

Chapter 3 supporting information VI Taxonomic groups and correlation coefficient of the calculated index variables for different types of forests 128

Chapter 3 supporting information VII Number of forest plots of the Biodiversity Exploratories in different forest types and regions 135

Chapter 3 supporting information VIII Ranges of species richness within individual taxonomic groups that were sampled in the Germany Biodiversity Exploratories and correlated with the FSI 136

Chapter 4 supporting information I (taken from chapter 2) 137

Chapter 4 supporting information II Histograms of FSI distribution for whole forest area of SW-Germany at NFI_{2002} and NFI_{2012} 137

Chapter 4 supporting information III Boxplots for analysed types of forests in SW-Germany illustrating the influences of harvesting intensities 138

Chapter 4 supporting information IV Changes of individual variable ranges ('variable-range_NFI_{2012}' – 'variable-range_NFI_{2002}') with increasing HI 143

Chapter 4 supporting information V Changes of individual variables applied in the FSI (y-axis: change of variable ranges; x-axis: classes for HI of 10%-intervals (0 – 100%), referred to standing volume at NFI_{2002}), for all analysed types of forests 147

Chapter 4 supporting information VI Changes of applied variables in the FSI with increasing HI for all analysed forest types; x-axis: increasing HI in 10% intervals of NFI_{2002} standing volume; y-axis: change of variable range........ 152

List of Figures

Figure 1.1. Relationship between structure, composition and function for ecosystem services in forests, adapted from Noss (1992). 4
Figure 1.2. Possible changes in structural and species diversity caused by increasing harvesting intensity; red line: no change, black line: negative change, blue line: optimal curve with positive influences of harvesting until a certain threshold is reached beyond which the influence becomes negative. Currently, these different relationships must be viewed as alternative hypotheses. 7
Figure 1.3. Main steps followed in this study to analyse the influence of harvesting intensities on structural and species diversity of forests. 9
Figure 2.1. Sampling grid of NFI_{2002} and NFI_{2012} in Baden-Württemberg, Germany 26
Figure 2.2. Frequency distribution of scores of the forest structural diversity index (FSI) for the second (NFI_{2002}) (left, mean = 0.18) and third (NFI_{2012}) national forest inventory (right, mean = 0.21)... 32
Figure 2.3. Change in scores of individual variables of the structural diversity index of Baden-Württemberg from the second to the third national forest inventory 34
Figure 2.4. Beanplots of FSI distributions in different forest types – left half of beans represents NFI_{2002} and the right half of beans represents NFI_{2012} 35
Figure 3.1. German Biodiversity Exploratories located in three regions of Germany............ 56
Figure 3.2. Density distribution of the Forest Structure Index (FSI) across 150 sampling plots of 1ha size of the Biodiversity Exploratories 60
Figure 3.3. Examples for correlations between structural diversity and species richness in the case of birds (left; cor: 0.54, R: 0.29) and deadwood fungi (right; cor: 0.38, R: 0.15)............ 61
Figure 3.4. Overview of correlations between FSI-score and species richness of taxonomic groups for three different stand development phases 63
Figure 4.1. Previous studies analysed differences in structural diversity between harvested and unharvested forests 79
Figure 4.2. FSI-scores of NFI_{2002}, (light grey bars) and NFI_{2012}, (dark grey bars) for different forest types of SW-Germany 83
Figure 4.3. Boxplots for changes of the Forest Structure Index and harvesting intensity (in % of standing timber volume per ha of NFI_{2002}, depicted in 10%-intervals), based on inventory data for the entire forest area of Baden-Württemberg... 84
Figure 4.4. Changes in ranges of individual variables contributing to the FSI with harvesting intensity for national forest inventory plots from Baden-Württemberg.................................. 85
Figure 4.5. Relative changes in values for individual variable ranges of the structural diversity index for plots with no harvesting activity (HI = 0) in the most recent inventory period (recorded) for whole Baden-Württemberg.. 86
Figure 4.6. Boxplots for young (left, stand development phase 1 (mean DBH ≤ 20 cm)) and middle-aged stands (right, stand development phase 2 (mean DBH between 20 and 50 cm)) 86
Figure 5.1. Sampling design of the GBE (inventory plot of 1 ha size) and angle-count samplings of the German NFI (variable in size) 101
Figure 5.2. Boxplots for changes of the FSI; highlighted number (x-axis) indicates average harvesting intensity for the period NFI_{2002} – NFI_{2012} 104

List of Tables

Table 2.1. Strengths and weaknesses of large-scale forest inventories such as the German NFI to assess surrogates for biodiversity based on forest structural diversity................................ 24
Table 2.2. Aspects of structural diversity and references for publications, in which the ecological rationale for the relevance of the different aspects of structural diversity for forest biodiversity are provided.. 28
Table 2.3. Core variables used in the Forest Structure Index and their recognized importance for biodiversity of forests 29
Table 3.1. Overview of applied data-sets and IDs of the German Biodiversity Exploratories to assess the performance of the FSI referred to different TGs... 57
Table 3.2. Variables of forest structure, which are used in the forest structure index, and the aspects of forest structure they represent 58
Table 3.3. Equations and examples to calculate the structural diversity index (FSI) at the plot level for forest stands in the German Biodiversity Exploratories 59
Table 3.4. Overview of correlation coefficients for relationships among species richness of selected taxonomic groups and individual variables of the structural diversity index for all plots of the German Biodiversity Exploratories... 63
Table 3.5. Correlations of individual variables used to calculate the FSI and the taxonomic group of birds for all regions and types of forests of the exploratories 65
Table 4.1. Tested models to explain the relationship between harvesting intensity (HI) and changes in structural diversity... 81

List of Abbreviations

BBW-ForWerts	Bioeconomy Baden-Württemberg - Erforschung innovativer Wertschöpfungsketten (exploring innovative value chains)
BW	State of Baden-Württemberg, SW-Germany
DFG	Deutsche Forschungsgesellschaft
FSI	Forest Structure Index
GBE	German Biodiversity Exploratories
HI	Harvesting intensity
NFI_{2002}	National Forest Inventory of Germany in 2002
NFI_{2012}	National Forest Inventory of Germany in 2012
TGs	Taxonomic groups

Publications and Contributions of Co-authors

Chapter 2 is published in the journal *Forest Ecosystems* and chapter 3 and 4 are prepared as manuscripts to be published in peer-reviewed scientific journals. Below, I will describe the contribution of each author. Further people that contributed to these three chapters are acknowledged in detail in each manuscript.

Chapter 2: *Storch F, Dormann CF, Bauhus J (2018) Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. Forest Ecosystems, 5(1), 34.*

Chapter 3: *Storch F, Dormann CF, Tschapka M, Gossner M, Fischer M, Feldhaar H, Boch S, Daniel R, Kaiser K, Wubet T, Karsten U, Polle A, Ammer C, Schall P, Weisser W, Bauhus J (to be submitted): Linking structural- to species-diversity of forests: An index based-approach.*

Chapter 4: *Storch F, Dormann CF, Kändler G, Bauhus J (to be submitted): Assessing the influence of harvesting intensities on structural diversity of forests in SW-Germany.*

I planned and conducted these three studies including the analysis and wrote the majority of the manuscripts. Jürgen Bauhus conceived and guided these studies and co-wrote the manuscripts. Carsten Dormann guided the statistical analysis in R that was applied in this study.

Summary

Most forests in Baden-Württemberg and Germany are managed, among other objectives, for the production of timber. In Germany and the EU there is a strong political direction towards a more bio-based economy to decrease the reliance on fossil fuels and to reduce the emissions caused by using fossil fuels and energy-intensive materials. Accordingly, policies and strategies have been developed to promote the use of bio-based materials. Currently, most biomass used for the bioeconomy is being harvested from forests. The increasing demand could lead to intensified harvesting of woody biomass from existing forests. This has raised concerns about possible impacts on biodiversity of forests. The influence of forest harvesting on biodiversity is difficult to assess in a comprehensive way and is typically only done in experiments or case studies. Hence there is no information for the total forest area of any given region, because we do not have a consistent monitoring of forest biodiversity. Instead of measuring different elements of biodiversity directly, it is possible to use the structural diversity of forests, which indicates the diversity of habitats, as a surrogate. This approach was used in this study to develop a tool that could be used to address future impacts and to identify thresholds of harvesting intensity that cause little or no harm on forest structural diversity.

On basis of the second National Forest Inventory of Germany for the state of Baden-Württemberg (NFI_{2002}), this project developed an index (FSI: Forest Structure Index) to assess the level of structural diversity. To include as many aspects of structural diversity in forests as possible, this index was calculated using eleven variables that were derived from this set of forest inventory data and cover important aspects of structural diversity. The many variables sampled in the NFI of Germany allow an assessment of different structural aspects, which are required to quantify structural diversity. The result was an assessment of the presence / absence or expression of structural elements and thereby structural diversity across many sites. The FSI was also calculated for NFI_{2012} and changes over a period of ten years (2002 – 2012) were analysed for different types of forests. The results show that NFI data of Germany and other countries with similar types of inventories can be used to calculate an index to describe structural diversity of forests; most of the important aspects of structural diversity can be derived from NFI data and were included in the FSI. Some aspects such as information on the litter-layer or microhabitats, however, remain excluded. The results show an increase in structural diversity for most of the analysed types of forests for the period 2002 – 2012, only young stand development phases showed a decrease of structural diversity (chapter 2).

While there are always some taxonomic groups (TGs) that are related to particular structural attributes, we don't know whether the whole range of different taxonomic groups in forests is actually related to the suite of structural attributes. To assess how well the FSI captured the variation in occurrence of forest-dwelling species I calibrated the index of structural diversity against comprehensive data on forest biodiversity. These data were available from the German Biodiversity Exploratories, where many different taxonomic groups (like birds, bats, vascular plants, bryophytes, lichen, fungi and different groups of insects) were measured on the same forest plots. For some of the tested taxonomic groups (e.g. the group of birds and deadwood fungi), the overall FSI-score can be used to successfully describe the presence / absence of species or the diversity of TGs across different types of forest stands. In addition, knowledge about important structural elements for individual tested TGs can be gained by analysing the correlation with single variables of the index. Subsequently taxon-specific indices could be developed on this basis. Some TGs were related to the structural diversity index only in single regions or in particular types of forest stands. Variation within a third class of TGs (e.g. orthoptera and hymenoptera) was not explained by the performance of the FSI. Here, either other structural elements may be important for the habitat of these taxonomic groups, or they may be more dependent on the abiotic environment or management related aspects (chapter 3).

In a third step, harvesting intensities for the period 2002 - 2012 were calculated on the basis of NFI data and combined with changes of the developed index at the plot-level. For this purpose, the influence of increasing harvesting intensities in different types of forests were analysed and recommendations for suitable harvesting intensities, regarding the maintenance of structural diversity, were made. This calculation was based on 10%-classes for harvesting intensities. This was necessary because the NFI of Germany uses the angle-count sampling method for many tree-related variables and hence plot information is not representative for the forest stands in which it was sampled. The influence of harvesting intensity on changes in the structural diversity index between inventory periods was therefore aggregated to form larger classes such as forest types or different stand development phases to produce more reliable and plausible results. These results show that some types of forests are influenced more negatively by increasing harvesting intensities than others. For all forest types analysed, except young stand development phases, a slight increase in structural diversity as expressed by the developed diversity index, was found for the period 2002 – 2012. Harvesting removals in this period were less than the biomass increment, indicating that future harvesting could theoretically be intensified without a loss in structural diversity, especially in conifer-dominated stands (mainly middle-aged spruce-dominated stands). Broadleaf-dominated forest stands show less potential for increasing harvesting intensity before a loss in structural diversity will be observed (chapter 4).

With this structural diversity index, originally developed for the large-scale forest inventory data of Baden-Württemberg, an assessment of structural diversity can be performed. Changes over 10-year periods can be analysed and recommendations for suitable harvesting intensities at the level of forest types can be developed. Results of our study show the potential for using structural variables of forests, derived from large-scale inventory data of Germany, to describe species diversity of some tested taxonomic groups like birds or deadwood fungi. As a next step, the potential for predicting the presence or diversity of single taxonomic groups by structural elements and their expressions on inventory plots could be examined, such as where data on species is missing, and to extrapolate this information to a larger scale.

So far, a tool to assess the level of structural diversity across many sites has been missing. The FSI developed in this study can be used to support decision making processes or societal debates on the use of forests. In general, harvesting activities do not necessarily influence the level of structural diversity negatively. In some types of forests, low harvesting intensities can even have slightly positive effects on structural diversity and thereby also on species diversity. These results indicate the possible increase in harvesting intensity in some types of forest stands and the amount of additional harvested woody biomass from existing forests could be used to support a growing bioeconomy sector in Baden-Württemberg or Germany.

Zusammenfassung

Die meisten Wälder Baden-Württembergs werden bewirtschaftet, um neben der Bereitstellung von holziger Biomasse auch weitere Leistungen abzudecken. Andauernde politische und wirtschaftliche Diskussionen deuten auf eine Veränderung hin zu einer stärker bio-basierten Wirtschaft, um sowohl die Abhängigkeit von fossilen Energien zu reduzieren, als auch die Emissionen dieser Stoffe zu verringern. Entsprechend wurden Gesetze entwickelt, um die Verwendung bio-basierter Materialien zu fördern. Derzeit wird der größte Teil der Biomasse, der durch die Bioökonomie verwendet wird, aus existierenden Wäldern bereitgestellt.. Der steigende Bedarf könnte zu einer verstärkten Nutzung der existierenden Wälder führen. Diese verstärkte Nutzung könnte sich auf die Biodiversität in Wäldern auswirken. Doch der umfassende Einfluss der Holznutzung auf Biodiversität ist schwierig zu ermitteln. Dies wurde bisher nur experimentell oder in Fallstudien untersucht. Daher gibt es keine Informationen über die Biodiversität für die gesamte Waldfläche, da kein einheitliches Monitoring-System vorhanden ist. Anstatt verschiedene Elemente der Biodiversität zu messen, kann die strukturelle Diversität von Wäldern als Ersatz für Biodiversität verwendet werden, welche die Vielfalt an unterschiedlichen Habitatstrukturen aufzeigt.

Dieser Ansatz wurde in der folgenden Untersuchung verwendet, um ein Werkzeug zu entwickeln, welches Auswirkungen der Holzernte erfasst und Grenzwerte für Nutzungen ausweist, die keinen oder lediglich geringen Einfluss auf strukturelle Diversität haben.

Um die strukturelle Vielfalt in Wäldern zu erfassen, wurde, auf Grundlage der zweiten Bundeswaldinventur Deutschlands ein Index (FSI = Waldstrukturindex) für das Bundesland Baden-Württembergs (BWI_{2002}) entwickelt. Um möglichst viele Bereiche der strukturellen Vielfalt zu erfassen, wurde dieser Index mit 11 Variablen berechnet, welche aus der Bundeswaldinventur abzuleiten sind und bedeutende Bereiche der Strukturvielfalt in Wäldern abdecken. Die zahlreichen Variablen, die in der BWI aufgenommen werden, ermöglichen eine Bewertung verschiedener struktureller Bereiche, was eine Voraussetzung ist, um strukturelle Vielfalt umfassend zu beschreiben. Das Ergebnis ist eine Aussage über das Vorhandensein / Fehlen oder die Ausprägung von Strukturelementen und damit struktureller Diversität über unterschiedliche Waldtypen hinweg. Der FSI wurde ebenfalls für unterschiedliche Waldtypen zum Zeitpunkt der BWI_{2012} berechnet, um somit Veränderungen über eine Periode von 10 Jahren zu untersuchen. Ergebnisse zeigen, dass BWI-Daten Deutschlands und weiterer Länder mit ähnlichen Waldinventuren verwendet werden können, um einen Index zu berechnen, mit dem strukturelle Vielfalt mehr oder weniger umfassend beschrieben werden kann. Die meisten der bedeutsamen Bereiche der Strukturvielfalt können

aus der Bundeswaldinventur abgeleitet werden und wurden im FSI verwendet. Lediglich wenige Bereiche, wie z.B. Informationen über die Streuauflage oder Mikrohabitate, konnten nicht berücksichtigt werden.

Die Ergebnisse zeigen einen Anstieg der strukturellen Vielfalt in den meisten untersuchten Waldtypen in der Periode 2002 – 2012; lediglich in jungen Bestandesentwicklungsphasen konnte ein Rückgang der strukturellen Vielfalt beobachtet werden (Kapitel 2).

Bisher lag der Fokus auf struktureller Vielfalt in Waldökosystemen. Während es immer taxonomische Gruppen (TGs) gibt, die mit einzelnen Strukturelementen verbunden sind, wissen wir nicht, ob die ganze Spanne an TGs in Wäldern mit der Auswahl an Strukturvariablen des Index erfasst wird. Deshalb war es notwendig, den entwickelten Strukturindex mit umfangreichen Biodiversitätsdaten zu kalibrieren. Diese Daten wurden durch die deutschen Biodiversitätsexploratorien zur Verfügung gestellt, in denen viele unterschiedliche TGs auf den gleichen Inventurpunkten untersucht wurden. Für manche der getesteten Gruppen (z. B. die Gruppe der Vögel und der Totholzpilze) konnte der Indexwert genutzt werden, um das Vorhandensein / Fehlen oder die Vielfalt über alle getesteten Waldtypen hinweg zu bestimmen. Zudem kann Wissen darüber generiert werden, welche Strukturvariablen des Index mit unterschiedlichen TGs korrelieren. Auf dieser Grundlage können nachfolgend taxon-spezifische Indizes entwickelt werden. Weitere TGs korrelierten nur in einzelnen Regionen oder Waldtypen mit dem Strukturindex. Die Vielfalt einer dritten Gruppe an TGs (z. B. Orthoptera oder Hymenoptera) konnte nicht durch den FSI erfasst werden. Dies kann entweder damit erklärt werden, dass weitere Strukturelemente von Bedeutung sind, welche nicht im FSI enthalten sind oder dass abiotische Umweltbedingungen oder Management-bezogene Aspekte für die Vielfalt dieser TGs von Bedeutung sind (Kapitel 3).

In einem dritten Schritt wurden auf Inventurpunkt-Ebene die Ernteintensitäten für die Inventurperiode 2002 – 2012 bestimmt und mit Veränderungen des Strukturindex kombiniert. Somit wurden Einflüsse steigender Ernteintensitäten in verschiedenen Waldtypen analysiert, um auf dieser Grundlage Empfehlungen für geeignete Ernteintensitäten, bezogen auf den Erhalt der Strukturvielfalt, zu geben. Diese Berechnung basiert auf 10%-Klassen für Nutzungsintensitäten, um die Anzahl der Inventurpunkte zu erhöhen und damit die Aussagekraft zu verbessern, was bei Inventuren wie der BWI notwendig ist, die teilweise die Methodik der Winkelzählprobe verwenden. Der Einfluss der Ernteintensität auf Veränderung des Strukturindex wurde auf Inventurpunkt-Ebene berechnet und dann zu größeren Einheiten wie Waldtypen oder einzelnen Bestandesentwicklungsphasen aggregiert. Ergebnisse zeigen, dass manche Waldtypen durch steigende Nutzungsintensitäten negativer beeinflusst werden als andere. Mit Ausnahme der jungen Bestandesentwicklungsphasen konnte für alle untersuchten Waldtypen ein leichter Anstieg der strukturellen Vielfalt, dargestellt durch den entwickelten Strukturindex, in der Periode 2002 - 2012 beobachtet werden. Die Entnahme an holziger Biomasse war geringer als der Zuwachs in dieser Periode, was auf eine theoretische Erhöhung der Erntemenge hinweist ohne die strukturelle Vielfalt zu reduzieren; insbesondere Nadelbaum-dominierte Bestände (hauptsächlich Fichten-dominierte Bestände mittleren Alters) zeigen eine mögliche Intensivierung der Nutzungen, bevor ein Rückgang an struktureller Vielfalt einsetzt. Laubwälder zeigen ein geringeres Potential die Erntemengen zu erhöhen bevor ein möglicher Rückgang der Strukturvielfalt erfasst werden kann (Kapitel 4).

Mit diesem Strukturindex, der ursprünglich für Großrauminventuren wie die Bundeswaldinventur entwickelt wurde, ist es möglich, die strukturelle Vielfalt von Wäldern zu bewerten. Veränderungen über 10-Jahres Perioden können untersucht werden um Empfehlungen zu angemessenen Erntemengen für größere Auswertungseinheiten wie z. B. Waldtypen zu entwickeln. Ergebnisse unserer Untersuchungen zeigen die Möglichkeit mittels Strukturvariablen, die aus Großrauminventuren in Wäldern abgeleitet werden können, die Artenvielfalt mancher taxonomischen Gruppen, wie beispielsweise die Gruppe der Vögel oder der Totholzpilze, über unterschiedliche Auswertungseinheiten erfolgreich zu beschreiben. In einem nächsten Schritt sollte die Möglichkeit untersucht werden, die Anwesenheit oder die Vielfalt einzelner taxonomischer Gruppen durch Strukturelemente und deren Ausprägung auf Inventurpunkten vorherzusagen, für die keine Informationen bezüglich dieser TGs vorhanden sind, um dieses Wissen auf große Flächen zu extrapolieren.

Bisher fehlte ein Werkzeug, um die strukturelle Vielfalt für verschiedene Waldtypen und Regionen zu erfassen. Der entwickelte FSI kann verwendet werden, um Entscheidungsprozesse oder gesellschaftliche Debatten über forstliche Nutzungen zu unterstützen. Generell beeinflussen Holzernten die strukturelle Vielfalt in Wäldern nicht zwangsläufig negativ. In manchen untersuchten Waldtypen konnte durch geringe Ernteintensitäten die strukturelle Vielfalt und damit auch die taxonomische Vielfalt / Biodiversität leicht erhöht werden. Diese Ergebnisse deuten auf eine mögliche Intensivierung der Holzernte in manchen Waldtypen hin, diese zusätzliche Menge an holziger Biomasse könnte verwendet werden, um eine wachsende Bioökonomie in Baden-Württemberg und Deutschland zu unterstützen.

1. General Introduction
1.1 The role of forests in the bioeconomy

One of the main problems of industrialized societies is the dependency on fossil energies, which are nowadays more limited than ever before. This limitation in resources as well as the supply or processing of these materials (e.g. coal mines or oil production) can have negative impacts on biodiversity and the planet. At the same time, the use of fossil fuels is the main driver of climate change. To counteract these negative impacts, the proportion of renewable energies, generated from wind farms increased in the last years (Federal Ministry for Environment, Nature Conservation and Nuclear Safety, 2012) and a financial incentive, for example, to promote solar energy was provided by the government of Germany (European Union, 2009).

To reduce the reliance on the fossil resource base and to find sustainable solutions for these problems, the field of bioeconomy was established. Here, different research fields and new processing methods are combined to develop new products and to reduce fossil energy demand to support the development towards a 'greener economy' for the world. But there are also critical studies questioning the implementation of bioeconomy in a sustainable way. For example, a successful realisation also requires a change in human behaviour and demands (as Smolker (2008) argued 'if we simply substitute plant biomass energy in place of fossil fuel energy, we are doomed'). Bouget *et al.* (2012) found negative impacts of fuelwood harvesting on biodiversity in Europe, which might be increased by the need of woody biomass for a growing bioeconomy, additionally. Kraxner *et al.* (2017) argued that Germany has to import timber already to cover its demands on woody biomass and a further increase of harvesting intensity will impact negatively on biodiversity of forests. In 2012, the European Commission adopted the strategy 'Innovating for Sustainable Growth: A Bioeconomy for Europe' (European Commission, 2012). This strategy suggests a comprehensive approach to address the ecological, environmental, energy, food supply and natural resource challenges that Europe and the world are facing in a sustainable way. These challenges include:

- increasing populations that must be fed
- depletion of natural resources
- impacts of ever increasing environmental pressures
- climate change

It has been postulated that a strong bioeconomy might help Europe to live within its limits. 'The sustainable production and exploitation of biological resources will allow the production of more from less, including from waste, while limiting negative impacts on the environment and reducing the heavy dependency on fossil resources, mitigating climate change and moving Europe towards a post-petroleum society' (European Commission, 2012).

Germany is one of the bioeconomy pioneers in the world (BMBF, 2014).The political strategy 'Bioeconomy in Germany' addresses these challenges and considers whether ecological and economic decisions can be combined in a sustainable way to face limitations of resources and to improve individual processing steps in an ecological and sustainable way.

Within the bioeconomy-sector, woody biomass will be the most important raw material for further utilisation steps (e.g. Pülzl *et al.* 2017). A planed cascade utilisation will allow multiple usages of timber products. For example, instead of burning, as mostly done at the moment with low quality timber, this material could undergo more value adding in a bioeconomy through a more targeted separation of different ingredients of wood (fibre, lignin, etc.) or conversion to bio fuel. Some chemical compounds might be used directly in industry processes like for example the 'green' Fischer-dowels, which are made of more than 50 % renewable materials or clothes and shoes made from newly developed bio-based compounds, as well as food based on micro-algae to secure the nutrient supply of humans. Using this comprehensive approach, a successful implementation might be possible to partially cover declining availability of fossil resources over the next few decades.

In 2013, the state of Baden-Württemberg, Germany founded the bioeconomy strategy 'Bioökonomie im System aufstellen' (The Ministry of Science, Research and the Arts of the State of Baden-Württemberg 2013), including the graduate programme 'BBW-ForWerts' (**B**ioeconomy **B**aden-**W**ürttemberg – Er**for**schung innovativer **Werts**chöpfungsketten) to explore a possible implementation strategy for the economic sector based on resources produced in this state. The declared goals of the bioeconomy are a) multiple utilisation of products (cascade utilisation) and b) to improve the individual utilisation steps of renewable energies (e.g. McCormick & Kautto, 2013, The Ministry of Science, Research and the Arts of the State of Baden-Württemberg, 2013). The programme contains 4 research areas (biogas, lignocellulose, microalgae, modelling as well as accompanying research in social sciences and ecology). The project, which forms the basis of this PhD thesis and analyses the influence of harvesting intensity on structural- and species-diversity in forests is part of the research area 'lignocellulose'. Further information about bioeconomy research in Baden-Württemberg, the participants and the variety of research topics can be found at https://biooekonomie-bw.uni-hohenheim.de/.

In Baden-Württemberg (BW), about 1.371 million hectare or 38.4 % of the state-area is covered by forests, illustrating the importance of forests for society. The average standing timber volume of 377 m³ ha^{-1} in BW is higher than the average of Germany (336 m³ ha^{-1}) and most forests are available for the production of timber products (Kändler & Cullmann, 2014). Although most forests were managed intensely (more than 90 % of the increment was harvested in the period 2002 – 2012 (based on NFI calculations for the state of BW)), the standing timber volume increased over the last few decades. This was mainly caused by relatively young forests and the high increment of these stand development phases. Mantau (2013, 2012) and Seintsch (2010) showed that the demand for woody biomass, extracted from forests, has been growing over the last few years in Germany. In particular, harvests of low quality timber have increased, which is mainly used for private burning. The new and growing bioeconomy sector might even enhance this trend by promoting the removal of additional large amounts of woody biomass, especially low quality timber, implementing cascade utilisation for chemical processes or as biofuel to counteract declining oil deposits and other fossil energies in future decades (McCormick & Kautto, 2013). This has raised concerns about the protection and conservation of biodiversity and other aspects of sustainable forest management (e.g. Gawel *et al.* 2018, Kraxner *et al.* 2017). Bioeconomy will not be able to solve any upcoming economic challenge but can contribute to counteract declining fossil energies by the development of sustainable alternatives in parts of the economic sector.

It has been suggested that - in theory - harvesting intensities in Baden-Württemberg for the use of wood as biofuel could be increased (Eltrop *et al.* 2006). In addition, harvesting rates of most types of timber are below their increment in the forest (Kändler & Cullmann 2014), which would allow an intensification of timber harvests. But this potential increase of harvesting intensities could impact negatively on biodiversity of forests (Bauhus *et al.* 2017). To support the protection of biodiversity and natural processes, about 10 % of the state-owned forest area remains unused (ForstBW, 2013). In state- owned and managed forests of BW, the support of rare and endangered species is implemented for example by the 'AuT-Konzept' (ForstBW, 2016), where groups of large trees and / or standing dead trees are excluded from harvests to provide rare habitat structures and thereby to directly support biodiversity in forests. A further example for implementation of habitat structures in forestry is provided by the 'Aktionsplan Auerhuhn' (Braunisch & Suchant 2013). Here, small forest areas have been harvested heavily to provide open forests combined with a certain vegetation type (e.g. blueberries), which are necessary for the presence of woodland grouse. This example demonstrates the possibility of influencing forest structure by management activities, mainly harvesting intensity or harvesting method, to support certain species directly.

1.2 Importance of structural diversity in forests

Protection and conservation of biodiversity, as part of forest management, is necessary to maintain healthy ecosystems (MCPFE 2003, Figure 1.1). 'Living forests are a basis of life on earth. By sustaining forests, we sustain life'. In forestry, structural elements like e.g. standing and downed deadwood, decay classes, species richness and dimensions of living trees can be used to assess the level of structural diversity (Bauhus & Pyttel 2015). Structural diversity is important for the diversity of taxonomic groups and by that for biodiversity (Lindenmayer *et al.* 2000, Noss 1990, Pielou 1975). Healthy ecosystems require a high level of biodiversity to provide ecosystem services like carbon storage, the presence of edible fruits and mushrooms or the provision of clear water and fresh air, as well as protection of soil, recovery of humans or nature conservation, which, beside the classical timber production, becomes more important nowadays (e.g. Plieninger *et al.* 2013, Hooper *et al.* 2005, Boyle 1992). These examples show the importance of structural diversity in forest ecosystems for the provision of ecosystem services.

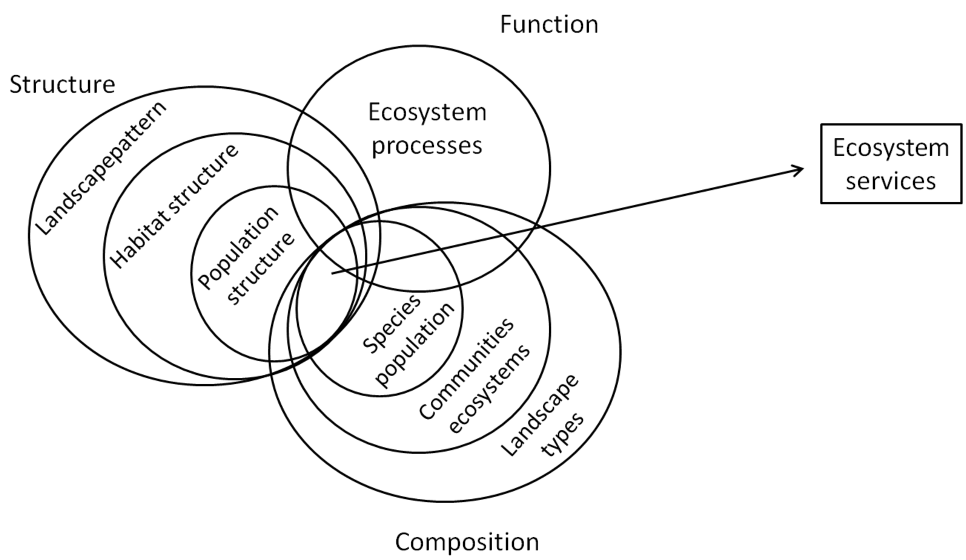


Figure 1.1. Relationship between structure, composition and function for ecosystem services in forests, adapted from Noss (1992).

This emphasise the need to protect and support biodiversity, especially in the cultural and heavily managed landscapes of Baden-Württemberg or Germany. However, in forestry and silviculture, the management of biodiversity is typically achieved through the management of structure and composition to provide a wide range of habitats or specific ones if it comes to the management of selected species. Therefore, structural elements like deadwood or large trees with habitat characteristics as well as the composition of forest stands are influenced and controlled as a surrogate for biodiversity, which underlines the importance of forest structure and its protection in forestry (Bauhus & Pyttel 2015). In addition, structurally and compositionally diverse forests may be more robust than monocultures or one-layered stands in relation to biotic and abiotic stress and disturbances (Bauhus *et al.* 2017, Thurm *et al.* 2016, Hooper *et al.* 2005). By providing several niches and structural elements like the presence of standing and downed deadwood, including different decay classes, a mixture of different tree species in several dimensions or the occurrence of large living trees as a surrogate for habitat tree characteristics like hollows, cracks or dead branches, a higher species diversity is assumed to be present (Lindenmayer *et al.* 2000, McCoy & Bell 1991). These diverse forest stands are required nowadays by many jurisdictions and suitable forest management strategies can be used to protect and also create these important structural elements. For example, harvesting methods like single tree fellings, group-wise fellings or clear cuts can have different influences on structural diversity (Kuuluvainen 2009, Rosenvald & Lohmus 2008, Siira-Pietikäinen *et al.* 2001). The deliberate protection and development of forest structural elements, also called retention forestry, can support the maintenance of populations of different species (Gustafsson *et al.* 2012, Bauhus *et al.* 2009, Abrahamsson & Lindbladh 2006).

So far, the influence of harvesting activities on structural diversity of forests has not been analysed across many sites. But these effects are the main reason for changes in forest structure, which may in turn influence biodiversity (Kuuluvainen 2009, Raison *et al.* 2001, Lindenmayer *et al.* 2000). Therefore, knowledge about these influences is required for different types of forests to analyse these relationships comprehensively. Previous studies compared the diversity of managed forests with the diversity of protected forests (e.g. Greenwood *et al.* 2017, Marchetti *et al.* 2017, Winkel *et al.* 2015) but the impacts of different harvesting intensities on structural diversity at a large scale have not been analysed. Paillet *et al.* (2010) showed that some taxonomic groups (e.g. bryophytes, lichen, fungi and saproxylic beetles) are affected more negatively by forest management than others (like e.g. the group of vascular plants or different bird species).

One of the goals of forest management is the protection of biodiversity, including structural elements of forests as well as the diversity of taxonomic groups (MCPFE, 2003). To protect biodiversity comprehensively, alpha-, beta- and gamma-diversity must be included but is not possible on existing data sets across many sites.

However, sampling of individual taxonomic groups (TGs) can be difficult, expensive and time consuming (Gardner 2010, Lindenmayer & Franklin 2002). This difficulty can be caused, for example, by taxon-specific characteristics like large home-ranges, seasonal appearances or expensive sampling efforts. Therefore, a surrogate in the form of structural elements could be used for the monitoring of biodiversity. Most of the existing studies focus on specific taxonomic groups (e.g. Leston *et al.* 2018, Watson *et al.* 2001) or were limited to small regions (Sabatini *et al.* 2015). A further approach to assess species diversity is through the sampling of indicator species (e.g. Fleishman *et al.* 2005). These indicator species represent a range of associated taxonomic groups. A prominent example in forestry is the sampling of woodpeckers as an indicator for the presence of the different species that they prey on and thus also for the habitat requirements of these prey species, e. g. the presence of standing deadwood (Mikusiński *et al.* 2001). By sampling the presence / absence or the diversity of these species, statements about the associated taxonomic groups (and / or habitat structures) can be possible for small areas. But this approach of using indicator species as a surrogate for biodiversity of forests has not been widely successful because of a lack of consistent correlations between the indicator species and the occurrence or abundance of other species (Duelli & Obrist 2003, Margules *et al.* 2002, van den Meersschaut & Vandekerkhove 2000).

As previous studies have shown, high structural diversity at the scale of forest stands can lead to high species- or taxonomic-diversity (‘habitat heterogeneity hypothesis’ e.g. Brunialti *et al.* 2010, Tews *et al.* 2004, Simpson 1949). In addition, a mixture of forest stands differing in structural diversities at the landscape level can also enhance taxonomic diversity, because some species and TGs are bound to low structural diversity in forests (Sullivan & Sullivan 2001, Okland 1996, Ralph 1985). A mixture of different even-aged forests at the landscape level had positive effects on species diversity, indicating that a combination of different stands with limited structural diversity can have positive impacts on the diversity of species at the landscape scale that exceed those of a landscape composed of structurally rich but very similar stands (Schall *et al.* 2018).

1.3 Structure and research questions of this thesis

This study aimed at assessing the influence of harvesting intensities on structural diversity in different types of forests (Figure 1.2) and at providing recommendations for harvesting intensities regarding the maintenance of structural diversity in forests.

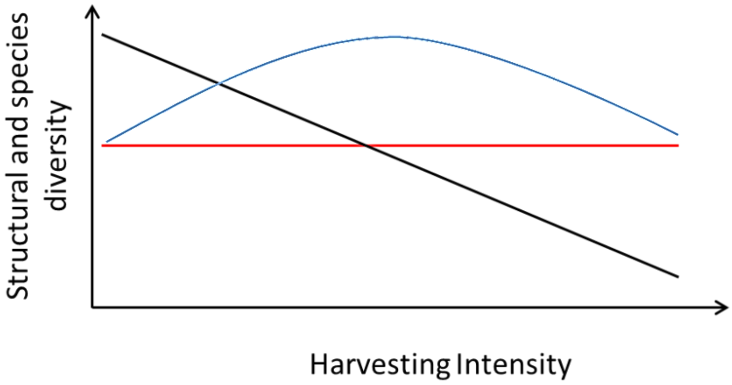


Figure 1.2. Possible changes in structural and species diversity caused by increasing harvesting intensity; red line: no change, black line: negative change, blue line: optimal curve with positive influences of harvesting until a certain threshold is reached beyond which the influence becomes negative. Currently, these different relationships must be viewed as alternative hypotheses.

A link from structural-diversity to species-diversity and by that to biodiversity has not previously been made across many sites. In some studies, sampling of taxonomic groups has been performed in small regions (e.g. Watson *et al.* 2001) but knowledge about the presence / absence has to be extrapolated to a large-scale to support species monitoring and the protection of habitat resources. Further studies compared managed forests and protected forests to analyse the impacts of forest harvesting on diversity (e.g. Greenwood *et al.* 2017, Marchetti *et al.* 2017, Winkel *et al.* 2015), excluding the possibility that harvesting intensities or methods could have different influences on the diversity of forests. As shown in Figure 1, knowledge about possible changes of structural diversity, which are mainly caused by increasing harvesting intensities, has to be gained if protection of structural diversity and thereby biodiversity should be implemented in forestry.

In this approach (Figure 1.3)

- I analysed the possibility of using large-scale forest inventory data of the German NFI_{2002} to assess the level of structural diversity in a standardised way for about 13.000 existing sampling plots in Baden-Württemberg.

- The second research question analyses the option to describe the presence / absence of different taxonomic groups using the structural elements of forests.
- The third research question analyses how different harvesting intensities cause changes in structural elements in forests.

Depending on these influences for the period 2002 – 2012, recommendations for future harvesting intensities can be provided for different types of forest stands.

Based on the literature, important structural elements were identified to describe structural diversity. This information was combined in a single index for structural diversity and calculated at the plot-level of the NFI. A set of inventory plots was needed to improve the accuracy of the index results derived from the sampling method applied in the NFI. Therefore, assessments of structural diversity were made at the forest-type level. To link structural diversity and diversity of taxonomic groups, the developed index was calibrated using biodiversity-data, provided by the German Biodiversity Exploratories. This data includes information about presence / absence or the diversity of many taxonomic groups, sampled on 150 inventory plots in different types of forests as well as forest inventory data that are necessary for the calculation of the FSI. Knowledge about habitat demands of different TGs, expressed by structural variables applied in the index and derived from this analysis, can be used to extrapolate information about important habitat structures across many sites where no information about diversity of taxonomic groups is available. As NFI-plots are sampled periodically (10 year periods – NFI_{2002} and NFI_{2012}), changes in the structural diversity index and thereby changes in habitat qualities can be calculated. Since harvests, in addition to broad-scale natural disturbances such as wind throw, are the main reason for changes of structural diversity, harvesting intensity was calculated from the NFI-data and related to changes in the index.

Therefore, an inventory period of 10 years (2002 - 2012) was applied to analyse the changes of structural diversity in forests, caused by different harvesting intensities and to gain knowledge about the impacts of harvests related to biodiversity. This underlines the importance of this analysis for the protection of biodiversity in upcoming decades. Harvesting intensity was calculated as the percentage of the standing volume of NFI_{2002} on the plot level and then aggregated in 10% classes to improve the data basis and the quality of the result; for example: standing volume at NFI_{2002}: 300 $m^3\ ha^{-1}$, harvested volume of the period 2002 – 2012: 100 $m^3\ ha^{-1}$ leads to a harvesting intensity of 33%.

To capture the impacts of timber harvests on structural diversity, a tool to measure diversity was developed based on National Forest Inventory data of Germany. Based on the results for individual types of forest stands, an assessment on previous harvests, as well as theoretical potentials of harvestable timber without a loss in structural diversity can be performed, which is still missing across many sites. Besides further limitations, these results cover an important aspect for the sector of bioeconomy in BW to calculate the potential of harvestable timber for the bio-economic utilisation in future decades.

Using this information, impacts of different harvesting intensities on structural diversity were analysed across many sites. To improve the accuracy of the index, harvesting intensities were calculated in 10%-steps of the standing timber volume of NFI_{2002}, to analyse the impacts of increasing harvesting intensities separately. Based on this knowledge, recommendations towards suitable harvesting intensities, related to the maintenance of structural diversity, can be made for different forest ecosystems in Baden-Württemberg or Germany. To comprehensively analyse the influence of harvesting intensity on structural- and species-diversity, three steps were necessary:

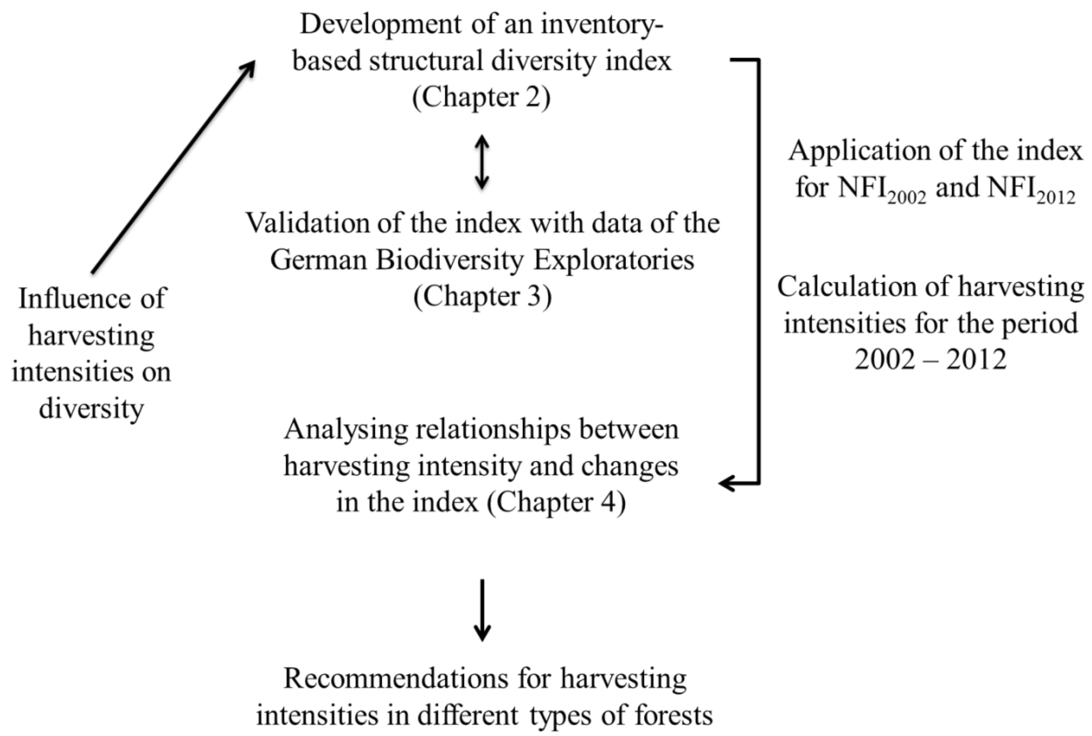


Figure 1.3. Main steps followed in this study to analyse the influence of harvesting intensities on structural and species diversity of forests.

Chapter 2 describes the development of a structural diversity index for forests in the state of Baden-Württemberg on the basis of large-scale inventory data, adapting an approach originally developed by McElhinny *et al.* (2006), supplemented by additional aspects of forest structure (Sabatini *et al.* 2015). Based on the literature, 11 aspects of structural diversity that could be derived from data of the German National Forest Inventory were identified as crucially important. Starting with a comprehensive list of candidate variables, these were reduced to one variable for each aspect of structural diversity using several selection criteria. This resulted in eleven variables, which were subsequently combined into a single index value by linking each value to a score. This index was calculated for each sampling point of the inventory (plot-level) and then aggregated to larger sampling units such as forest types. This chapter was also submitted to the Journal *Forest Ecosystems* in May 2018 and is now under revision.

The aim of *chapter 3* was to assess, whether the index of the structural diversity of forest stands actually explained variation in the presence or abundance of forest-dwelling species. It only makes sense to use the index for the monitoring of forest biodiversity, if these relationships exist. For that purpose, the index for structural diversity was calculated for 150 plots of the German Biodiversity Exploratories (DFG project, see Fischer *et al.* 2010) and its performance was compared to the presence / absence or diversity of taxonomic groups found on this plots. For a first group, the overall index values showed robust correlations with the presence / absence of some taxonomic groups over all analysed types of forests. Diversity of a second group showed correlations with the index in singles types of forests and a third group was not described by the calculated index. These results show the heterogeneity in demands for habitat structures of different taxonomic groups, which are only partly covered by the developed index. For the correlated groups, the overall FSI-score could be used to assess habitat quality using structural elements of forests. This chapter is being prepared for publication in the Journal *Forest Ecology and Management*.

In *chapter 4*, we tested the sensitivity of the index to harvesting intensity. To estimate the impacts of different harvesting intensities on structural diversity of forests, changes in the index were related to harvesting intensities of the inventory period 2002 - 2012. Results showed a heterogeneous picture: some types of forests were intensively harvested in this period and a further increase would reduce the diversity of forest structural elements. For other types of forests, harvesting intensity could be increased before a significant loss in biodiversity would occur. This knowledge can be used to recommend future harvesting intensities in order to maintain the level of diversity in different types of forests.

The results of my PhD research show that it is possible to assess the structural diversity of forests, derived from large-scale inventory data. Based on eleven variables, an index to measure the level of structural diversity was developed and applied to different types of forests stands. Changes in this structural diversity index over periods of 10 years can be calculated easily but a second inventory-period would be needed to capture long-term changes as well as instant changes and thereby assess the influence more comprehensively. A prediction of species diversity from structural diversity was tested for different taxonomic groups, as well as the overall diversity of these TGs in different types of forests. Results show that it is possible to describe the diversity of some TGs like birds or deadwood fungi using the overall index-score. In addition, knowledge about important variables for the presence of individual TGs can be derived from this study to develop taxon-specific indices, which are based on some of the 11 variables tested, combined with further area-specific variables like slope or altitude. Changes in this index, which are mainly caused by harvests were analysed for different types of forests to develop recommendations on harvesting intensities aiming at the maintenance or improvement of structural diversity. To support a growing bioeconomy sector with woody biomass, extracted from forests, the main source would be conifer-dominated stands, mainly middle-aged spruce-dominated stands that can be theoretically harvested more intensely than in the previous inventory period before a loss in structural diversity sets in.

1.4 References

Abrahamsson M, Lindbladh M (2006) A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (Picea abies). In: Forest Ecology and Management 226 (1-3), S. 230–237. DOI: 10.1016/j.foreco.2006.01.046.

Bauhus J, Kouki J, Paillet Y, Asbeck T, Marchetti M (2017) How does the forest-based bioeconomy impact forest biodiversity? In: Winkel, G (ed.) Towards a sustainable European forest-based bioeconomy – assessment and the way forward. What Science Can Tell Us 8, European Forest Institute, pp. 67-76. ISBN 978-952-5980-41-7

Bauhus J, Pyttel P (2015) Managed forests. In: Peh KSH, Corlett RT and Bergeron Y (eds.) Routledge Handbook of Forest Ecology. Routledge, Oxon, pp.75-90.

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. In: Forest Ecology and Management 258 (4), S. 525–537. DOI: 10.1016/j.foreco.2009.01.053.

BMBF (2014) Bioökonomie in Deutschland: Chancen für eine biobasierte nachhaltige Zukunft. https://www.bmbf.de/pub/Biooekonomie_in_Deutschland.pdf; 05.06.2018

Bouget C, Lassauce A, Jonsell M (2012) Effects of fuelwood harvesting on biodiversity - a review focused on the situation in Europe. Canadian Journal of Forest Research, 42(8), 1421-1432. Boyle TJB (1992) Biodiversity of Canadian forests: current status and future challenges. The Forestry Chronicle, 68(4), 444-453.

Braunisch V, Suchant R (2013) Aktionsplan Auerhuhn Tetrao urogallus im Schwarzwald: ein integratives Konzept zum Erhalt einer überlebensfähigen Population. Vogelwelt, 134, 29-41.

Brunialti G, Frati L, Aleffi M, Marignani M, Rosati L, Burrascano S, Ravera S (2010) Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. In: Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 144 (1), S. 221–233. DOI: 10.1080/11263500903560959.

Duelli P, Obrist MK (2003) Biodiversity indicators. The choice of values and measures. In: Agriculture, Ecosystems & Environment 98 (1-3), S. 87–98. DOI: 10.1016/S0167-8809(03)00072-0.

Eltrop L, Moerschner J, Härdtlein M, König A (2006) Bilanz und Perspektiven der Holzenergienutzung in Baden-Württemberg.

European Commission (2012) https://ec.europa.eu/research/bioeconomy/pdf/official-strategy_en.pdf; 05.06.2018

European Union (2009) Richtlinie 2009/28/EG des Europäischen Parlaments und des Rates vom 23. April 2009 zur Förderung der Nutzung von Energie aus erneuerbaren Quellen und zur Änderung und anschließenden Aufhebung der Richtlinien 2001/77/EG und 2003/30/EG https://eur-lex.europa.eu/legal-content/DE/TXT/PDF/?uri=CELEX:32009L0028&from=DE; 05.06.2018

Federal Ministry for Environment, Nature Conservation and Nuclear Safety (2012) Zeitreihen zur Entwicklung der erneuerbaren Energien in Deutschland.. https://www.erneuerbare-energien.de/EE/Redaktion/DE/Downloads/zeitreihen-zur-entwicklung-der-erneuerbaren-energien-in-deutschland-1990-2017.pdf?__blob=publicationFile&v=15

Fischer M, Bossdorf O, Gockel S, Hänsel F, Hemp A, Hessenmöller D (2010) Implementing large-scale and long-term functional biodiversity research: The biodiversity exploratories; Basic and Applied Ecology, 11 (2010), pp. 473-485

Fleishman E, Thomson JR, Mac Nally R, Murphy DD, Fay JP (2005) Using indicator species to predict species richness of multiple taxonomic groups. Conservation Biology, 19(4), 1125-1137.

ForstBW (Hrsg) (2016) Alt- und Totholzkonzept Baden-Württemberg. 44 Seiten, Stuttgart. http://www.forstbw.de/fileadmin/forstbw_infothek/ forstbw_praxis/ForstBW-PRAXIS_Alt-_und_Totholz_WEB.pdf; 04.06.2018

ForstBW (Hrsg) (2013) Gesamtkonzeption Waldnaturschutz, Stuttgart. http://www.forstbw.de/uploads/media/504-15_ForstBW_Broschuere_Gesamtkonzeption_Waldnaturschutz_01.pdf; 05.06.2018

Gardner T (2010) Monitoring forest biodiversity: improving conservation through ecologically-responsible management. Routledge.

Gawel E, Purkus A, Pannicke N, Hagemann N (2018) A Governance Framework for a Sustainable Bioeconomy: Insights from the Case of the German Wood-based Bioeconomy. In Towards a Sustainable Bioeconomy: Principles, Challenges and Perspectives (pp. 517-537). Springer, Cham.

Greenwood S, Jump A, Sotirov M, Marchetti M, Mikusinski G, Bastrup-Birk A, Brotons L, Hermoso V & Parviainen J (2017) Effectiveness of Natura 2000 in forests in EU-28. In: Sotirov M (ed.). Natura 2000 and Forests: Assessing the State of Implementation and Effectiveness. What Science Can Tell Us, 7, Joensuu, Finland: European Forest Institute, pp. 81-100.

Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, Lindenmayer DB, Lõhmus A, Martínez Pastur G, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney WJA, Wayne A, Franklin JF (2012) Retention Forestry to Maintain Multifunctional Forests: a World Perspective. Bioscience 62, 7, 633-645

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning. A consensus of current knowledge. In: Ecological Monographs 75 (1), S. 3–35. DOI: 10.1890/04-0922.

Kändler G, Cullmann D (2014) Der Wald in Baden-Württemberg. Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Forstliche Versuchs-und Forschungsanstalt Baden-Württemberg, Freiburg.

Kraxner F, Fuss S, Verkerk PJ (2017) Is there enough forest biomass available to meet the demands of the forest-based bioeconomy? In Towards a sustainable European forest-based bioeconomy (No. 8, pp. 53-65). European Forest Institute.

Kuuluvainen T (2009) Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe. The Complexity Challenge. In: AMBIO: A Journal of the Human Environment 38 (6), S. 309–315. DOI: 10.1579/08-A-490.1.

Leston L, Bayne E, Schmiegelow F (2018) Long-term changes in boreal forest occupancy within regenerating harvest units. In: Forest Ecology and Management. DOI: 10.1016/j.foreco.2018.02.029.

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity. A comprehensive multiscaled approach. Washington, DC: Island Press.

Lindenmayer DB, Margules CR, Botkin DB (2000) Indicators of biodiversity for ecologically sustainable forest management. Conservation biology, 14(4), 941-950.

Mantau U (2013) Auswirkungen der stofflichen und energetischen Nutzung auf den Waldholzverbrauch.

Mantau U (2012) Holzrohstoffbilanz Deutschland: Entwicklungen und Szenarien des Holzaufkommens und der Holzverwendung von 1987 bis 2015.

Marchetti M, Bastrup-Birk A, Parviainen J, Santopuoli G, Vizzarri M, Jump A, Sotirov M (2017) The state of biodiversity in Europe's forest systems.

Margules CR, Pressey RL, Williams PH (2002) Representing biodiversity. Data and procedures for identifying priority areas for conservation. In: J Biosci 27 (4), S. 309–326. DOI: 10.1007/BF02704962.

McCormick K, Kautto N (2013) The bioeconomy in Europe: An overview. Sustainability, 5(6), 2589-2608.

McCoy ED, Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. Habitat structure: the physical arrangement of objects in space (ed. By Bell SS, McCoy ED and Mushinsky HR), pp. 3–27. Chapman & Hall, London.

McElhinny C, Gibbons P, Brack C (2006) An objective and quantitative methodology for constructing an index of stand structural complexity. In: Forest Ecology and Management 235 (1-3), S. 54–71. DOI: 10.1016/j.foreco.2006.07.024.

MCPFE (2003) ‘Forest Summit Declaration‘ European Forests - Common Benefits, Shared Responsibilities". In *Fourth Ministerial Conference on the Protection of Forests in Europe* (pp. 28-30).

Mikusiński G, Gromadzki M, Chylarecki P (2001) Woodpeckers as indicators of forest bird diversity. Conservation biology, 15(1), 208-217.

Noss RF (1992) Issues of scale in conservation biology. In *Conservation biology* (pp. 239-250). Springer, Boston, MA.

Okland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation, 76, 297–310.

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Kanka R (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation biology, 24(1), 101-112.

Plieninger T, Dijks S, Oteros-Rozas E, Bieling C (2013) Assessing, mapping, and quantifying cultural ecosystem services at community level. Land use policy, 33, 118-129.

Pülzl H, Giurca A, Kleinschmit D, Arts B, Mustalahti I, Sergent A, Brukas V (2017) The role of forests in bioeconomy strategies at the domestic and EU level. In Towards a sustainable European forest-based bioeconomy (No. 8, pp. 36-53). European Forest Institute.

Raison RJ, Flinn DW, Brown AG (2001) Application of criteria and indicators to support sustainable forest management: some key issues. CAB International, 2001. In: In Criteria and (2001).

Ralph CJ (1985) Habitat association patterns of forest and steppe birds of Northern Patagonia, Argentina. The Condor, 87, 471–483.

Rosenvald R, Lohmus A (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management, 255(1), 1-15.

Sabatini FM, Burrascano S, Lombardi F, Chirici G, Blasi C (2015) An index of structural complexity for Apennine beech forests. In: iForest 8 (3), S. 314–323. DOI: 10.3832/ifor1160-008.

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Buscot F (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology.

Seintsch B (2010) Holzbilanzen 2006 bis 2009 für die Bundesrepublik Deutschland. Johann Heinrich von Thünen-Institut.

Siira-Pietikäinen A, Pietikäinen J, Fritze H, Haimi J (2001) Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. Canadian Journal of Forest Research, 31(1), 88-99.

Simpson EH (1949) Measurement of diversity. Nature, 163, 688.

Smolker R (2008) The new bioeconomy and the future of agriculture. Development, 51(4), 519-526.

Sullivan TP, Sullivan DS (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology, 38, 1234–1252.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity. The importance of keystone structures. In: Journal of Biogeography 31 (1), S. 79–92. DOI: 10.1046/j.0305-0270.2003.00994.x.

The Ministry of Science, Research and the Arts of the State of Baden-Württemberg (2013) Bioökonomie im System aufstellen (Stuttgart 2013) https://www.baden-wuerttemberg.de/fileadmin/redaktion/dateien/PDF/Broschuere_Konzept-baden-wuerttembergische-Forschungsstrategie-Biooekonomie.pdf; 05.06.2018

Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. In: Forest Ecology and Management 376, S. 205–220. DOI: 10.1016/j.foreco.2016.06.020.

Van den Meersschaut D, Vandekerkhove K (2000) Development of a stand-scale forest biodiversity index based on the State Forest Inventory.

Watson J, Freudenberger D, Paull D (2001) An Assessment of the Focal-Species Approach for Conserving Birds in Variegated Landscapes in Southeastern Australia. In: Conservation Biology 15 (5), S. 1364–1373. DOI: 10.1111/j.1523-1739.2001.00166.x.

Winkel G, Blondet M, Borrass L, Frei T, Geitzenauer M, Gruppe A, Winter S (2015) The implementation of Natura 2000 in forests: A trans-and interdisciplinary assessment of challenges and choices. Environment.

Chapter 2: Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring

Examples for structural diversity in forests:

a) structural poor even-aged spruce (*Picea abies* L.) stand (*), b) structural rich mixed-stand (*), c) downed deadwood with different decay classes (*), d) standing deadwood (*), e) large tree with habitat characteristics (*)

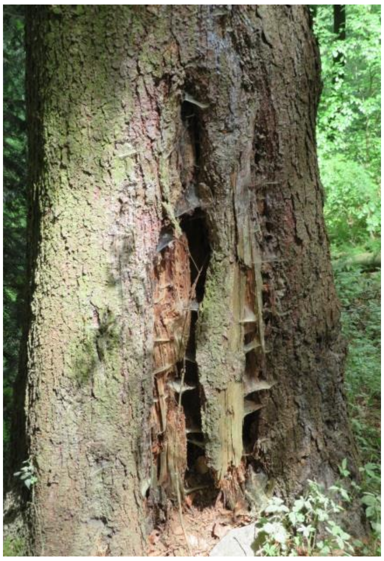
a)

b)

c)

d)

e)



(*): pictures taken by Felix Storch

Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring

Felix Storch[1], Carsten F. Dormann[2] and Jürgen Bauhus[1]

[1] Chair of Silviculture, University of Freiburg, D-79085 Freiburg, Germany

[2] Chair of Biometry, University of Freiburg, D-79085 Freiburg, Germany

Author for correspondence

Felix Storch

Tel: +49-(0)761-203-8628

Fax: +49-(0)761-203-3781

Email: *felix.storch@waldbau.uni-freiburg.de*

Key words: *stand structure, structural diversity, structural diversity index, large-scale forest inventory, angle count sampling*

This chapter was published in the journal *Forest Ecosystems*, September 2018 and is available at https://doi.org/10.1186/s40663-018-0151-1

Citation: Storch F, Dormann CF, Bauhus J (2018) Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. *Forest Ecosystems*, *5*(1), 34.

2.1 Abstract

The importance of structurally diverse forests for the conservation of biodiversity and provision of a wide range of ecosystem services has been widely recognised. However, tools to quantify structural diversity of forests in an objective and quantitative way across many forest types and sites are still needed, for example to support biodiversity monitoring. The existing approaches to quantify forest structural diversity are based on small geographical regions or single forest types, typically using only small data sets. Here we developed an index of structural diversity based on National Forest Inventory (NFI) data of Baden-Württemberg, Germany, a state with 1.3 million ha of diverse forest types in different ownerships. Based on a literature review, 11 aspects of structural diversity were identified a priori as crucially important to describe structural diversity. An initial comprehensive list of 52 variables derived from National Forest Inventory (NFI) data related to structural diversity was reduced by applying five selection criteria to arrive at one variable for each aspect of structural diversity. These variables comprise 1) quadratic mean diameter at breast height (DBH), 2) standard deviation of DBH, 3) standard deviation of stand height, 4) number of decay classes, 5) bark-diversity index, 6) trees with DBH ≥ 40 cm, 7) diversity of flowering and fructification, 8) average mean diameter of downed deadwood, 9) mean DBH of standing deadwood, 10) tree species richness and 11) tree species richness in the regeneration layer. These variables were combined into a simple, additive index to quantify the level of structural diversity, which assumes values between 0 and 1. We applied this index in an exemplary way to broad forest categories and ownerships to assess its feasibility to analyse structural diversity in large-scale forest inventories. The forest structure index presented here can be derived in a similar way from standard inventory variables for most other large-scale forest inventories to provide important information about biodiversity relevant forest conditions and thus provide an evidence-base for forest management and planning as well as reporting.

2.2 Introduction

2.2.1 The importance of forest structural elements for biodiversity monitoring

Structurally diverse forests are important to maintain species-rich communities (Brunialti *et al.* 2010, Taboada *et al.* 2010, Simpson 1949). MacArthur & MacArthur (1961) showed for example, that diversity of birds can be stronger influenced by vertical heterogeneity of forest stands than by composition of tree species. A higher diversity of bark characteristics (shapes and expressions) can lead to higher species diversity by provision of different microhabitats (Michel *et al.* 2011, Woinarski *et al.* 1997, Recher 1991). Lassauce *et al.* (2011) found that diversity of saproxylic organisms in boreal forests is strongly correlated with volume and decay classes of deadwood and Bouget *et al.* (2013) recommended the diversification of deadwood (types of deadwood, diameter and length, decay classes, etc.) as a management tool for saproxylic beetles in deciduous forests.

Over the last decades, forest management approaches such as 'close-to-nature forestry' or 'retention forestry' have been recommended to improve habitat provision through an increase in quantities of structural elements such as deadwood and large old trees (Bauhus *et al.* 2013, Gustafsson *et al.* 2012). For practical implementation, this means extending rotation periods, retaining trees with microhabitat features, increasing deadwood volume and even creating standing dead trees and high stumps artificially (e.g. Bauhus *et al.* 2009, Abrahamsson & Lindbladh 2006, Ranius *et al.* 2005). While there is a reasonably good research foundation for these measures, there is only scant documentation about their effectiveness in routine forestry. Yet in many jurisdictions, forest owners, in particular public forest authorities, are requested to monitor biodiversity and report on their management efforts to maintain or improve biodiversity. There is, as yet, no established or accepted monitoring approach for different types of ecosystems (Noss 1990, Pielou 1975). In addition, biodiversity is extremely difficult and very expensive to monitor (Gardner 2010, Lindenmayer & Franklin 2002). This is caused by a range of factors including species-specific characteristics like large home-ranges or seasonal appearances, even when the focus is 'only' on species richness or even only on endangered species. The approach of using indicator (key) species as a surrogate for biodiversity of forests has not been widely successful because of a lack of consistent correlations between the indicator species and the occurrence or abundance of other species (Duelli & Obrist 2003, Margules *et al.* 2002, van den Meersschaut & Vandekerkhove 2000).

For those reasons, comprehensive approaches to monitor forest biodiversity comprising many different taxa have so far not been implemented in regular forest inventories.

In the context of forests, the main influence of management on biodiversity is through changes in forest structure and composition (Kuuluvainen 2009, Raison *et al.* 2001, Lindenmayer *et al.* 2000), where structure and composition are commonly deliberately manipulated to achieve certain ecosystem functions and services (Bauhus & Pyttel 2015, Plieninger *et al.* 2010). Thus it appears logical to monitor changes in these important determinants of biodiversity in the absence of direct data on forest species and their populations and genetic variation (Taboada *et al.* 2010). The monitoring of biodiversity relevant aspects of forest structure and composition may be integrated into standard forest inventories at little additional cost when compared to separate approaches for biodiversity monitoring (Corona 2016).

2.2.2 Existing indices on structural diversity of forests

Several indices estimating structural diversity of forests have been described in the literature. Some focus on specific structural elements such as deadwood (Larsson 2001) or have been developed to assess specific habitat attributes of different species or species groups (e.g. '*Structural Complexity Index*' for small mammals (Barnett *et al.* 1978) or '*Habitat Complexity Score'* for assessment of bird habitats (Watson *et al.* 2001)). Others have been developed for particular geographical regions and focus mainly on one tree species or stand type ('*Structural Heterogeneity Index*' (Sabatini *et al.* 2015)). Indices such as the '*Old-Growth Index*' (Acker *et al.* 1998) are related to structural diversity of old-growth stands, assuming the highest level of diversity to be found there. The '*Austrian Forest Biodiversity Index*' is based on a relatively subjective set of variables derived from Austrian National Forest Inventory (NFI)-data (Geburek *et al.* 2010).

A comprehensive, quantitative index of structural diversity was developed by McEhinny *et al.* (2006) using a reproducible approach underlined by statistical analysis. In their approach, a comprehensive list of candidate variables was reduced to those that capture the variability of the different structural aspects best through Principal Component Analysis. This approach was modified and applied in our analysis to develop an index of structural diversity. In general terms, structural diversity may be described by many different variables, or these may be combined into a single index value (e.g. McElhinny et al. 2006) as is also the case for other environmental indicators and indices (Niemeijer and de Groot 2008). One advantage of using a set of variables is the more detailed information about individual structural elements and their changes over inventory periods. This more detailed information may be required for the monitoring of certain aspects of structural diversity that are related to ecosystem functioning or habitat quality of particular taxonomic groups. This monitoring-oriented focus on individual aspects of structural diversity is particularly relevant for multipurpose forest management and planning (e.g. Corona 2016). The disadvantage of this approach is that it is less suitable for reporting purposes, especially for non-expert audiences. An aggregation of structural variables into a single index value facilitates reporting levels of structural diversity and their development over time in broad terms to a general audience including non-governmental organisations and decision makers. In that sense, such an aggregated index of forest structural diversity is similar to a ‘state indicator’ of the ‘pressure, state, response’ concept of environmental indicators proposed by the OECD (2003). Here we combined these two approaches. On the one side, we identified individual structural variables that may be related to specific aspects of forest biodiversity and that may respond differently to forest management. On the other side, we combined these individual variables into a single number for an index of structural diversity to facilitate communication of changes in forest structure at a high level of information aggregation, for example to facilitate policy processes and decision making.

2.2.3 Large-scale inventories to support biodiversity monitoring

So far, large-scale inventories have been rarely used to determine the level of structural diversity (Polley 2010, Kändler 2006). However, valuable information about diversity of forests can be obtained as a ‘byproduct’ of existing inventory data and therefore at low costs (Corona *et al.* 2011, Corona *et al.* 2003). One advantage of such an inventory is the wide range of sampled forest attributes. Yet these types of NFI were originally not developed to capture forest structure but the main reason for the development and implementation was to analyse the development of forest growing stock and the available amounts of different types of forest products. However, the information demand gradually increased and hence additional variables with high relevance for the quantification of forest structure were included. For example, in the NFI_{2002}, variables related to biodiversity and carbon storage such as deadwood (dimensions, decay classes, types of deadwood) or regeneration were added. ‘Hollow trees’, as well as other habitat-tree characteristics (very old trees or crown deadwood) were added in the NFI_{2012}.

The large area covered as well as the number of sample plots used in the inventories allows quantification of structural diversity for different forest types. An overview of strengths and weaknesses of the applied large-scale inventory for the assessment of structural diversity is provided in Table 2.1.

Table 2.1. Strengths and weaknesses of large-scale forest inventories such as the German NFI to assess surrogates for biodiversity based on forest structural diversity.

strengths	weaknesses
Large number of inventory plots for different strata such as jurisdictions or biogeographical regions and broad forest types	Sampling based on angle count method; only a selection of trees are sampled, which leads to a loss of information at the plot-level (probability proportional to size)
Approach applicable to NFIs of other countries	The large-scale design (2 X 2 km grid) does not capture effectively small areas like forest reserves
Adequate number of sampling plots per forest type available (for main forest types, see supporting information V, chapter 2)	Biodiversity-relevant variables were originally not included in inventory-samplings; increasing integration of biodiversity-relevant variables only in recent inventories (NFI_{2002} and NFI_{2012})
Low costs for acquisition of data that are attached to or can be derived from classical inventory variables	No precise information about harvesting and other management activities at the plot-level
Dynamic changes over inventory periods can be considered (ongoing process)	Changes in sampled variables and sampling thresholds between NFIs (e.g. threshold-value for the minimal diameter for downed deadwood or the presence of hollows)
Same plots are (re)sampled → Analysis on changes of structural elements and development of individual trees (over periods of 10 years)	While broad forest types can be analysed, local (regional) aspects may not be sufficiently well represented
A large number and variety of structural variables can be derived from inventory data	Owing to the sampling method and related small radius of sampling circles, plot measures are not representative of the stand in which they were collected; therefore extrapolation to hectare values is problematic
	Some important variables of forest structure are not quantified directly. They can only be addresses through surrogates (e.g. the occurrence of large living trees as surrogate for habitat-tree characteristics)

Based on NFI data, indices of forests structural diversity may be developed. This could permit the quantification of levels of structural diversity in different forest types, as well as its changes over inventory periods (e. g. 10 years). Subsequently these changes may be related to other inventory information such as harvesting intensity. Indices that are based on standard inventory variables may be transferred to other large-scale forest inventories and thus facilitate assessments of structural diversity over large areas within or across jurisdictions (Chirici *et al.* 2011, Corona *et al.* 2011).

2.2.4 Study aims

The main goal of this study was to explore the potential of large-scale forest inventories to assess forest structural diversity and its development over time using an objective and quantitative way to support biodiversity monitoring (Table 2.1). Based on the successful development of an index of structural diversity, we present, in an exemplary form, information on the status and development of structural diversity in different forest types of Baden-Württemberg, Germany.

2.3 Material and Methods

Data of two National Forest Inventories of Germany for the state of Baden-Württemberg (NFI_{2002} and NFI_{2012}) were used for this study. The inventory design was based on a systematic sampling grid of 2 x 2 km for the state of Baden-Württemberg, which has a denser grid than most other states with 4 x 4 km. In the north-east corner of each grid intersection point, up to 4 permanent sampling plots (1 - 4) were marked invisibly (if located in forest areas) at a distance of 150 m to each other. In Baden-Württemberg, about 12.920 forest plots were sampled at both inventories and used in this analysis.

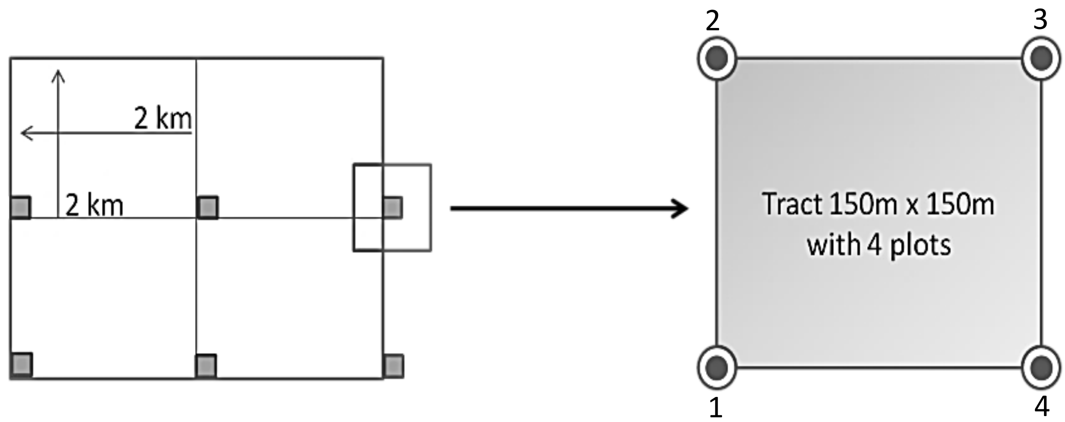


Figure 2.1. Sampling grid of NFI_{2002} and NFI_{2012} in Baden-Württemberg, Germany

At each sampling plot, a combination of sampling methods was used to collect forest stand attributes (supporting information I of chapter 2). The complete sampling design and further information about the inventory can be found at BMBL (2013) <https://www.bundeswaldinventur.de>.

To construct an index of structural diversity of forests ('FSI' = Forest Structure Index), we adopted and improved the method developed by McElhinny *et al.* (2006). This approach consisted of 4 steps:

1. Defining aspects of structural diversity. Based on a literature review and the information derivable from NFI data, 11 aspects of structural diversity were identified to be represented in a comprehensive index. 2. Establishing a comprehensive list of structural variables derived from National Forest Inventory data (measured in both NFI_{2002} and NFI_{2012}) that are related to the above aspects of structural diversity. Each variable belongs to one aspect of structural diversity (Table 2.2, see also Sabatini *et al.* 2015). 3. Reducing the number of variables to a core set of structural attributes by applying the following five selection criteria: a) distribution of data for the different variables should cover as much as possible the potential range of values and be as even as possible; unlike McElhinny *et al.* (2006), who used kurtosis as a criterion to assess the distribution of data for each variable, here the distribution was assessed visually. Testing the distribution of variables was mandatory because variables with wide spread and / or evenly distributed data are most suitable for this analysis. Variables with highly skewed data distributions or rare observations were not appropriate, because they would likely not be able to discriminate between different levels of structure across the plots; b) the variable functions as a surrogate for other variables of the same aspect; c) continuous variables are better suited than categorical variables (aggregation in classes leads to a loss of information, enhanced by subjective class limits); d) all aspects of structural diversity must be included in the index (Table 2.2); e) the variable shall be a non-compound measure, excluding for example Shannon-like indices which amalgamate richness and abundance. 4. Combining core variables into a simple additive index, scored relatively to observed maxima in NFI_{2002}.

The information provided by core variables had to be transferred and combined into a single index-score to express the overall level of structural diversity in forests and hence to allow the assessment of temporal changes over a period of time (development) or comparisons among different forest types. If NFI-values were assumed to include extreme values (caused by the sampling method) or implausible measurements, ranges of possible minimum and maximum values for the respective variables were used, based on NFI_{2002} data or literature. All variables showing higher values than the threshold-value were reduced to the maximum score of 1. Thereby, the loss of information was very small, because only few sampling plots were affected. An overview of the applied threshold-values is provided in supporting information II of chapter 2.

The equation to calculate variables-scores:

$$Variable - Score = \frac{(X - Xmin)}{(Xmax - Xmin)}$$

'X' was the measured variable-value at plot-level and 'X_{min}' respectively 'X_{max}' were the minimum and maximum values observed in NFI_{2002} data for each variable.

The sum of scores of the core variables divided by the number of variables included in this index yields a value between 0 and 1, where 0 indicates 'lowest level of structural diversity' and 1 'highest level of structural diversity'. Multiplying variables to calculate an index value, as was done for example in the index developed by Geburek *et al.* 2010, was regarded as unsuitable in our case because it assumes that structural diversity is depending on the presence of all structural elements captured by the variables (Burgman *et al.* 2001). If a single variable had a value of zero, the complete index would be zero. Rejecting those zero-values from index calculations would solve this problem but prevent a further comparison of index-scores, if these are based on different numbers of applied variables. Therefore, we decided to follow an additive way to construct this index as described above. In theory, the individual variables of the index could receive a different weight according to their relevance for overall richness of habitats and associated species. Here, the index was calculated with unweighted variables because we had no prior information whether individual variables of forest structure were more or less important than others, e.g. for species richness within certain taxonomic groups. To test whether the assignment of different weightings to individual variables has a significant influence on the distribution of index values across inventory plots, a sensitivity analysis was performed, using for each variable random weightings between 0 and 2, which were repeated 100,000 times.

Finally, sampling plots were aggregated to forest types by different stand attributes like dominant tree functional type (broadleaf or conifer species), stand development phase, dominant tree species (beech, oak, spruce or pine), forest-ownership or number of canopy-layers. For these forest types, mean FSI-scores were calculated for both inventories and compared to each other, as well as among different types of forests. Thus, information was aggregated from the plot- to the forest-type level and a statement about the structural diversity as well as changes in structural diversity in forests representing large areas was possible. Microsoft Access 2010 was used to calculate variables, derived from NFI_{2002} and NFI_{2012}, describing structural diversity of forests. For further analysis, the statistic software R (Version 3.1.2) and its package beanplot was used for beanplots.

2.3.1 The study area

Almost 39% or 1.371 million ha of the area of Baden-Württemberg (SW-Germany) is covered by forests. To develop an index for structural diversity, 13.106 inventory plots of NFI_{2002} were used. By excluding plots that a) were without merchantable timber at the time of NFI_{2002}, b) experienced a change in land use (e.g. plot covered by forest at NFI_{2002} but converted into urban or agricultural land at NFI_{2012}), and c) that were not accessible at both inventory dates, 12.918 plots or 98.6% of all sampled forest plots remained for this analysis.

2.4 Results and Discussion

2.4.1 Aspects of structural diversity

In a first step, we identified through a broad literature review 11 aspects of structural diversity that should be included in a comprehensive index of forest structural diversity (FSI) (Table 2.2).

Table 2.2. Aspects of structural diversity and references for publications, in which the ecological rationale for the relevance of the different aspects of structural diversity for forest biodiversity are provided; see also Sabatini *et al.* (2015). The right column refers to the number of variables that can be derived from the National Forest Inventory in relation to this aspect. The complete list of these 52 variables is provided in the supporting information III. The aspects below the dashed line (‘litter layer’, ’microhabitats’, ’tree spacing’ and ‘growth on deadwood’) could not be considered in this analysis because they were not sampled by the NFI. Some ’microhabitats’ were only added to sampling during NFI_{2012}, so they could not be taken into account for this work.

Aspect of structural diversity	Acronym	Authors	Number of variables
Uneven-agedness	UA	Hatanaka *et al.* 2011, Keeton 2006	7
Growing stock	GS	Hoover *et al.* 2012, Norris *et al.* 2011, Houghton 2005	7
Compositional heterogeneity	CH	Hatanaka *et al.* 2011, Burrascano *et al.* 2011, Barbier *et al.* 2009, Barbier *et al.* 2008	5
Vertical heterogeneity	VH	Burrascano *et al.* 2013, Hao *et al.* 2007, Staudhammer & LeMay 2001	3
Large living trees	LLT	Brunialti *et al.* 2010, Persiani *et al.* 2010, Nilsson *et al.* 2002	3

Deadwood standing	DW st	Hatanaka *et al.* 2011, Brunialti *et al.* 2010	5
Deadwood downed	DW d	Zotti *et al.* 2013, Lassauce *et al.* 2011, Castagneri *et al.* 2010	8
Deadwood decay classes	DC	Lombardi *et al.* 2011, Lassauce *et al.* 2011, Burrascano *et al.* 2008	2
Bark diversity	BD	Michel *et al.* 2011, MacFarlane & Luo 2009, Bhadra *et al.* 2008	1
Diversity of flowering and fruiting trees	FD	Singh & Kushwaha 2005	1
Regeneration	REG	Müller *et al.* 2008, Boyden *et al.* 2005, Hello 1985	10
Litter Layer	LL	Watson *et al.* 2001, Newsome & Catling 1979, Gilmore 1985 (for habitats of birds), Barnett *et al.* 1978	0
Microhabitats	MH	Bütler *et al.* 2013, Michel *et al.* 2011, Winter & Möller 2008, Dueser & Shugart 1978	0
Tree Spacing	TS	Bachofen & Zingg 2001, Acker *et al.* 1998, Pretzsch 1997, Spies & Franklin 1991	0
Growth on deadwood (lichen, mosses, fungi)	DW G	Hoppe *et al.* 2016, Dittrich *et al.* 2014, Blaser *et al.* 2013, Humphrey *et al.* 2002	0

2.4.2 Core variables of structural attributes

After application of the above mentioned selection criteria, the following variables were identified as the most suitable to represent the corresponding aspect of structural diversity (Table 2.3). If reduction of variables resulted in more than one variable that was suitable to represent the aspect of structural diversity, a Principal Component Analysis (PCA) could be performed. To perform a PCA, distribution of variable-data must be approximately normal. In our study, this final step was not necessary because only one variable per aspect was considered as suitable for a further application in the index.

Table 2.3. Core variables used in the Forest Structure Index and their recognized importance for biodiversity of forests

Variable	Aspect	Author	Explanation
DBHq (quadratic mean diameter of trees (> 7 cm DBH) at breast height)	**GS** growing stock	Tanabe *et al.* 2001, Ziegler 2000, Ferreira & Prance 1999, Acker *et al.* 1998, Uuttera *et al.* 1997, Spies & Franklin 1991	Common variable to describe stand structure; higher DBHq implies older and taller stands with high biomass, typical forest microclimate, and more presence of habitat attributes of mature forests.
DBH sd (standard deviation of diameter at breast height of trees > 7 cm DBH	**UA** uneven-agedness	McElhinny *et al.* 2006, Neumann & Starlinger 2001, Acker *et al.* 1998	High standard deviation of DBH implies a diverse stand structure with patches of different densities and tree dimensions; many niches are provided for different taxa;

			relates to canopy layering
Height sd (standard deviation of mean height of trees > 7 cm DBH)	**VH** vertical-heterogeneity	Sabatini *et al.* 2015, McElhinny *et al.* 2006, MacArthur & MacArthur (1961)	Standard deviation of stand height describes the vertical heterogeneity of stands directly; relates to canopy layering
Bark (index to describe diversity of bark types)	**BD** Bark diversity	Bhadra *et al.* 2008, McElhinny *et al.* 2006, Eyre & Smith 1997, Pearce 1996, Dickman 1991, Gilmore 1985	Diversity of bark types (smooth, fissured, peeling, scaly, cracked, etc.) in forest stands implies a variety of habitats for many species to be found there (insects, fungi, yeasts, spiders, epiphytes). Tree diameter and bark-development phases are considered
Flower-diversity (diversity of fruiting and flowering trees)	**FD** Flower diversity	Singh & Kushwaha 2005, Herrera *et al.* 2001, Soderquist & MacNally 2000, Smith *et al.* 1994, Andrews *et al.* 1994, Kavanagh 1987	Food source for nectarivorous and frugivorous species (mainly insects, bats and birds)
VolTrees40 (volume per hectare of trees with a DBH ≥ 40cm)	**LLT** Large living trees	Larrieu & Cabanettes 2012, Ziegler 2000, Van Den Meersschaut & Vandekerkhove 2000, Acker *et al.* 1998, Tyrell & Crow 1994, Koop *et al.* 1995, Spies & Franklin 1991	Large trees have a special function as habitat or source of food for many taxa; they have a greater probability to provide microhabitat structures such as hollows, crown dead wood, etc.
N DC (number of decay classes)	**DW DC** deadwood decay classes	Dittrich *et al.* 2014, Blaser *et al.* 2013, Lachat *et al.* 2013, Lassauce *et al.* 2011	Important for many taxonomic groups; many decay classes indicate a continuous recruitment of deadwood; indicator for natural forest conditions
Deadwood mean DBH st (mean DBH of standing deadwood)	**DW s** standing deadwood	Lassauce *et al.* 2011, Drapeau *et al.* 2009, Verkerk *et al.* 2011, Rondeux & Sanchez 2010, Lachat *et al.* 2013	Important structural element for many taxa of xylobiotic species (habitat and food source); more suitable than volume/ha because of strong extrapolation effects when sampled on small plots; stumps are excluded from the calculation
Deadwood d average mean diameter (average mean diameter of downed deadwood)	**DW d** downed deadwood	Lassauce *et al.* 2011, Brin *et al.* 2011, Drapeau *et al.* 2009, Rondeux & Sanchez 2010, Verkerk *et al.* 2011, Kappes & Topp 2004, Lachat *et al.* 2013	Important structural element for many taxa of xylobiotic species (habitat, food source, regeneration niche); surrogate for deadwood types and N/ha of dead wood pieces, justified by level of correlation and better distribution

SR (richness of tree species with DBH ≥ 7cm)	**CH** compositional heterogeneity	Sullivan *et al.* 2001, Uuttera *et al.* 2000, Van Den Meersschaut & Vandekerkhove 2000, Maltamo 1997, Uuttera *et al.* 1997; Pretzsch 2005, Pretzsch 2003, Tilman 1999, Lähde *et al.* 1994	Species richness of trees with DBH ≥ 7cm is important for diversity of dependent species, in particular host-specific herbivores, detritivores, symbionts and pathogens
SR Reg (species richness of regeneration (DBH < 7cm))	**REG** regeneration	Warnaffe & Deconchat 2008, Müller *et al.* 2008, Mosimann *et al.* 1987	Important for many taxa like insects, mammals and birds; high SR Reg leads to more diverse future stand conditions

Even though some of these applied variables were closely correlated, we did not remove any of them for subsequent development of the index because they represented clearly different aspects of structural diversity. For example '*volume of trees ≥ 40 cm DBH'* (describing the aspect of large living trees) and '*species richness of trees with DBH ≥ 7 cm'* (describing compositional heterogeneity) were highly correlated. The correlations among different variables associated with a particular aspect of structural heterogeneity as well as correlations with other variables for the whole forest of Baden-Württemberg are listed in supporting information IV of chapter 2.

2.4.3 Scaling of variables to derive index values

Extreme values of variables (outliers), leading to scores higher than 1 were reduced to a score of 1 to maintain the data distribution unchanged and use the whole spectrum of data-variety for the analysis. The low values for downed deadwood, standing deadwood and number of decay classes (Figure 2.3) can be explained by the distribution of data for these variables, respectively the large number of sampling plots without deadwood or different decay classes. In addition, the small sampling plot for deadwood applied in the NFI (radius of 5 m), exacerbates this problem, because deadwood occurs often in a clumped distribution and is not equally distributed within forest stands, so the actual amounts of deadwood might not be recorded accurately.

2.4.4 Scaling up from plot to forest type-level

To aggregate information on structural diversity (FSI-score) from a plot- to a forest type-level, single plots were assigned to strata, here categories of forest types (related to NFI-classifications, e.g. ownership or number of canopy layers). It is important to work with larger forest types that are represented by an adequate number of sampling plots (Sterba 2008, Lappi & Bailey 1987) to obtain reliable results for the FSI (or information about the level of structural diversity). A table containing the different forest types and their corresponding number of inventory plots is provided in the supporting information V of chapter 2.

Some previously developed indices of structural diversity used individual weightings for variables (Geburek *et al.* 2010, Parkes *et al.* 2003). This can only be justified, if there is a clear rationale for valuing some variables more or less than others, i.e. if it was known that a certain aspect of structural diversity had a proportionally higher or lower influence on species richness or diversity. In our study, there were no obvious variables that should receive more or less weight than others in order to represent the overall forests biodiversity. Weighting of variables could be performed when the FSI is linked to individual taxonomic groups, because some elements of structural diversity that are crucial for one taxonomic group could lead to an absence of other taxonomic groups (Okland 1996). In addition, we tested the performance of the FSI using random weightings applied to the selected variables. The results of the sensitivity analysis, which used random weightings between 0 and 2 for each variable, show that the performance of the FSI was insensitive to weightings of variables ($R^2 = 0.97$, CV = 0.01), which were therefore not applied in routine calculations.

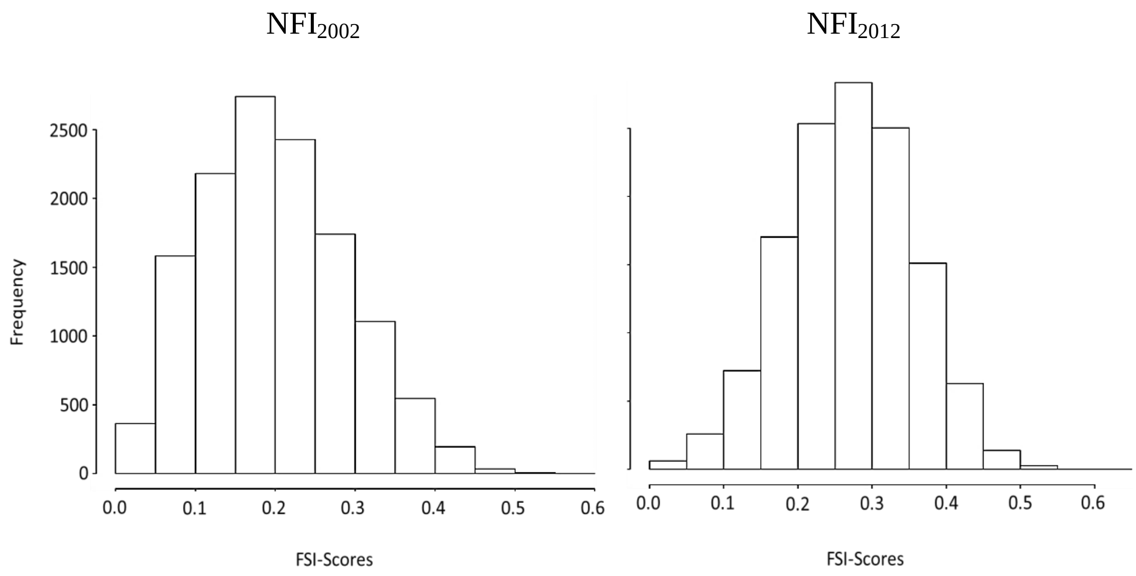


Figure 2.2. Frequency distribution of scores of the forest structural diversity index (FSI) for the second (NFI_{2002}) (left, mean = 0.18) and third (NFI_{2012}) national forest inventory (right, mean = 0.21). Scores were calculated for 12.918 inventory plots within Baden-Württemberg. Differences between NFI_{2002} and NFI_{2012} are significant for an applied confidence level of 0.95

The small number of plots with very high and very low FSI-values indicate that the developed index is potentially sensitive to the existing level of diversity of structural elements in forests of SW-Germany, which include a broad range of structural diversities (from intensively managed forests to strict reserves). In contrast, one-sided distributions for this diverse data-set would indicate that the FSI produces similar values for many sampling plots and was not sensitive enough to describe the diverse spectrum of structural diversity in forests. The histograms show a close to normal distribution and a broad range of FSI-scores, which represent different structural 'qualities' (from structurally poor to comparatively high levels of structural diversity; Figure 2.2). A maximum FSI-score of 1 is theoretically possible but very unrealistic in reality, because all applied variables must be present at their maximum expression. In addition, high scores for some variables might exclude high scores for other variables (e.g. high species richness (mixture of shade-tolerant and shade-intolerant species) might exclude high species richness in the regeneration layer, caused by missing shade-intolerant species). The highest FSI-score calculated on the basis of NFI_{2002}-data was 0.52, which represents the highest level of structural diversity in forest-plots of Baden-Württemberg. The lowest FSI-scores were found in young stand development phases and the highest FSI-scores are found in old broadleaf-dominated stands which are conform to general assumptions on the level of structural diversity in different stand development phases of managed forests (e.g. Scherzinger 1996, Spies & Franklin 1991, Bazzaz 1975). Distributions of the FSI scores for other categories of forests (e.g. broadleaf- / conifer-dominated, beech-, oak-, pine-, spruce-dominated, three stand development phases, ownerships or number of canopy layers) are provided in the supporting information VI of chapter 2.

A comparison of FSI scores for the NFI_{2002} and NFI_{2012} showed that the index is sensitive to temporal changes in forest structure and composition and that the scores increased for all individual variables contributing to the index, except standing deadwood decreased slightly (Figure 2.3).

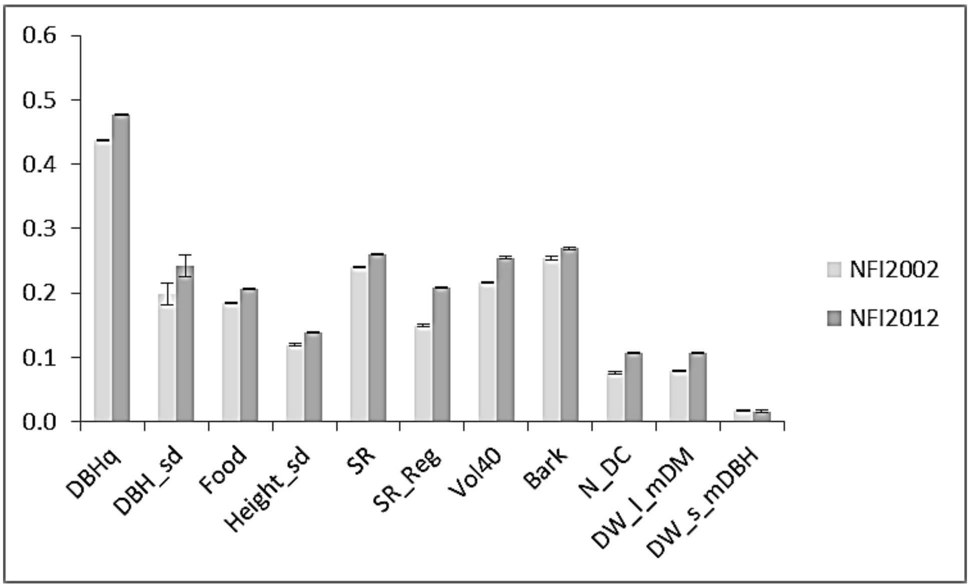
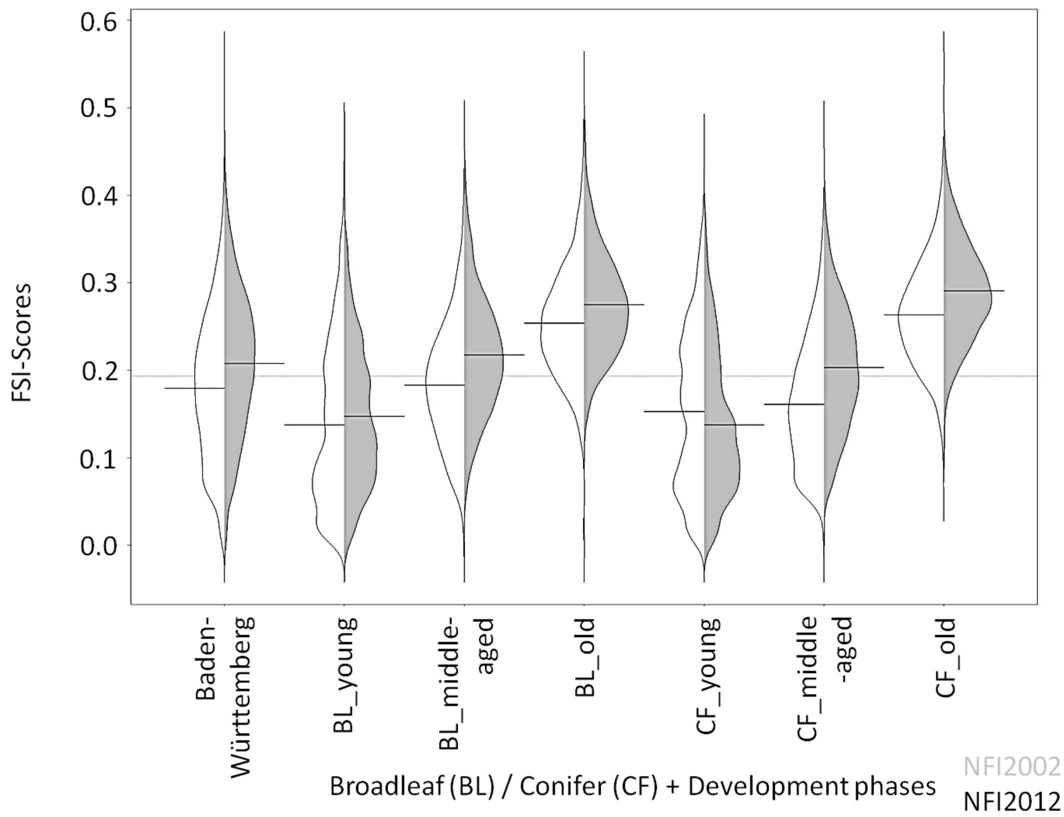


Figure 2.3. Change in scores of individual variables of the structural diversity index of Baden-Württemberg from the second to the third national forest inventory (NFI_{2002}, NFI_{2012}). Error bars represent standard error of means. Differences between NFI_{2002} and NFI_{2012} are significant for an applied confidence level of 0.95 for all applied variables.

The changes in the FSI for NFI data from Baden-Württemberg corresponded to results of the analysis of NFI-data for single variables (Figure 2.3). These showed a small general increase in all structural elements apart from standing deadwood for the period between NFI_{2002} and NFI_{2012}. In general, young stands had a lower structural diversity than middle-aged stands (Stand development phase 1 - FSI NFI_{2012} = 0.14; Stand development phase 2 - FSI NFI_{2012} = 0.21). Not surprisingly, the FSI score for NFI_{2012} indicated that one-layered stands (0.14) were less diverse than two- (0.21) or multi-layered stands (0.24). The highest level of structural diversity was observed in old stands (0.28), followed by multi-layered stands (0.24). For all analysed forest types, except for young and young-conifer dominated stands, an increase of structural diversity took place for the period NFI_{2002} – NFI_{2012}. The highest increase in structural diversity was found for stand development phase 2 and pine-dominated stands (0.04) (Fig. 2.4).



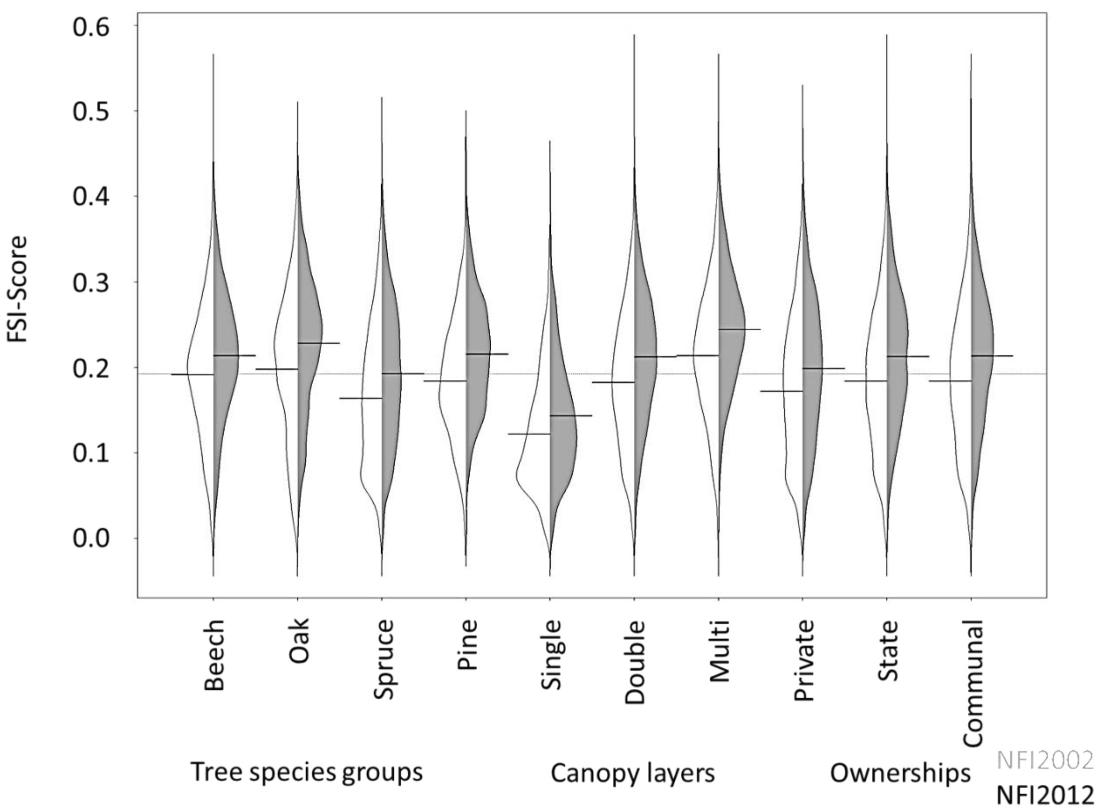


Figure 2.4. Beanplots of FSI distributions in different forest types – left half of beans represents NFI_{2002} and the right half of beans represents NFI_{2012}; direct comparison of FSI for

NFI_{2002} and NFI_{2012} per stand type as well as a comparison between different forest types; black lines indicate mean values of forest types; except of young conifer-dominated stands, all types of forests show an increase between the FSI-score for NFI_{2002} and NFI_{2012}. All types of forests show significant differences between the two NFIs (t-test, confidence level of 0.95).

2.4.5 Assessment of absolute FSI-scores

Expressing the level of structural diversity in a single number may yield questionable results, especially if several, quite different aspects of structure are combined in one index (Whitman & Hagan 2007). For example, a deadwood-rich but species-poor stand can receive the same index-score as a stand without deadwood but a more diverse diameter distribution or species richness. However, this ’hidden information’ of the FSI score can be made visible by depicting the changes in single FSI-variables (Figure 2.3). This variation in structural attributes behind similar FSI-values is an inevitable consequence of aggregation, but it is not per se unrealistic, because biodiversity is depending on many different structural aspects. If we assume that the different types and combinations of structural variables represent habitats for different taxa, then we can also expect quite different forest communities for similar FSI-scores.

In general, the FSI-score provides a standardised and transparent assessment of the overall diversity of large forest types. The highest FSI-score was found in old stands. In this type of forest, all variables included in the FSI, except for ‘quadratic mean diameter at breast height’, ‘standard deviation of diameter at breast height’, ‘occurrence of large living trees’ and 'Bark-diversity' assume approximately average values for forests in Baden-Württemberg. However, old stands scored significantly higher than the average for the above mentioned four variables, providing the underlying causes for the high overall FSI values in this forest type.

The adaption of NFIs to support biodiversity monitoring has developed over the last decades and is now more widely used. Additional variables for further information on deadwood or habitat trees, which are important to gain a comprehensive view on biodiversity in forests, have been included in the list of inventoried variables (Corona *et al.* 2011). Adaptations of threshold-values (for example changes in minimum sampled diameter of deadwood or threshold-diameter for large trees, which is used as a surrogate for habitat-trees) are easily possible in the FSI. This makes the FSI a flexible tool which can be adapted easily to inventory data from other types of forest ecosystems or other regions. In addition, variables that have not been sampled in past NFIs (of Germany) but provide information about further aspects of structural diversity can be included in the index, when data become available (e.g.

information about the litter layer or microhabitats, Table 2.2). This important information could be obtained in upcoming NFIs to further support biodiversity monitoring in a more comprehensive way and thereby improve the information value of the FSI.

A comparison between the performance of FSI and other indices describing structural diversity of forests based on inventory data (like Parkes *et al.* 2003, Denslow & Guzman 2000, Newsome & Catling 1979) was not possible in this study, because some variables required by these indices were not sampled in the NFI (e.g. 'canopy cover' or information about 'litter'). These other indices of stand structural diversity use variables that are not measured in most conventional forest inventories (e.g. litter decomposition, litter dry weight and thickness, number of hollow trees, amount of crown deadwood, swelling of trunk bases, species richness of small plants (shrubs or ground vegetation)), which would need to be collected in separate inventories that can be typically carried out only in specific forest types or regions. In contrast, the FSI presented here can be readily adapted to most other European large-scale National Forest Inventories, easily (e.g. Austria, Switzerland, Italy or Spain) because it uses variables that are measured in most European NFIs (Tomppo *et al.* 2010). In addition, it is possible to reduce the number of applied variables in the FSI (if some information is missing) because the aggregated score is calculated in a simple additive way and results are expressed in a relative instead of absolute numbers. However, the comparability of the FSI and its constituent variables with other inventories depends also on the sampling methods employed in the inventories.

2.4.6 Angle count sampling and transfer to different inventory methods

When using inventory data for a structural diversity index like the NFI of Germany, which is partly based on sampling via the angle count method, it is important to aggregate index-scores at a stratum level (e.g. forest type) (Sterba 2008, Lappi & Bailey 1987, Bitterlich 1948). Observations or changes of structural diversity for single inventory plots should not be considered because dramatic changes recorded at individual plots may be caused by the sampling design rather than by actual changes in forest structure. Observed differences in variables between two inventories at a single plot may be attributable to the method of PPS (probability proportional to size) sampling, that angle count sampling is based on. Whether a tree is included in the sample or not depends on its diameter at breast height and its distance to the centre of the inventory plot. The associated low number of trees leads, in most cases, to a loss of information at the plot-level (justified by the need to optimize the sampling effort).

For larger study areas and inventory strata, the accuracy of observations from angle count sampling is as high as that from inventories employing fixed radius circles (Lappi and Bailey 1987; Sterba 2008). On this basis, accurate calculations of harvested timber volume or biomass, growing stock, availability of certain products, etc. have been successfully performed in the past (Polley 2005; Kändler and Cullmann 2014; Polley and Kroiher 2017).

The low scores of deadwood-related variables of the FSI for Baden-Württemberg (deadwood standing, deadwood downed and deadwood decay classes, see Fig. 3) may be explained through the sampling of this attribute, which has a rare occurrence, on relatively small plots of 5 m radius (Meyer 1999; Ritter and Saborowski 2012). However, large amounts of deadwood, when scaled up to a hectare, can be recorded at individual plots (for example the highest value of downed deadwood (1713 m3·ha− 1) was the result of only two large trees sampled within the 5 m plot). Therefore, average mean diameter was chosen for downed deadwood, mean DBH for standing deadwood and number of decay classes for the aspect of decay classes. These variables did not have to be scaled up to hectare values and therefore delivered more accurate values than volume·ha− 1 or number·ha− 1. This problem (rare occurrence) may be exacerbated by the high threshold value for deadwood in NFI_{2002} (20 cm diameter at the large end). In addition, in most forest areas deadwood occurs in a clumped distribution. Hence single 5-m-radius plots are not sufficiently large to quantify dead wood representatively for entire stands (Ritter and Saborowski 2012). While this variability can normally be dealt with through aggregation of inventory plots to the level of sufficiently large strata to derive representative mean values (e.g. Lombardi et al. 2015), it leads to very high deviation of deadwood volumes determined at the plot level from the mean of the stratum, if dead wood volumes determined in one such plot are scaled directly to the hectare level. Similarly, the occurrence of other rare elements (like hollow trees, very large trees or rare tree species) is probably underestimated when compared to other inventory methods using larger fixed sampling plots. A transfer of the approach presented here to inventories using fixed radius circles, as they are used in other types of inventories appears to be possible, but further research has to be done on this topic, e.g. if an adaption of threshold-values for the applied variables is needed.

2.5 Conclusion

The main goal of this study was to assess the feasibility of an index of forest structural diversity based on large-scale forest inventory data to support biodiversity monitoring. Our results show that the index developed here provides an objective assessment of the status of structural diversity for different forest types and that it is sensitive to temporal changes. More detailed information about the level of structural diversity (single variables or their development over time) in different forest types can be derived. Our index of forest structural diversity can be readily adapted to other, similar types of national or regional forest inventories. The index of forest structural diversity developed here serves one of the major directions in recent developments of forest inventories towards multipurpose resources surveys, namely the incorporation of additional variables that are not directly related to traditional inventory purposes such as assessment of timber, wood volume increments or carbon stocks and sequestration (Corona 2016). However, the index has been derived from variables that are already measured in current forest inventories and hence it can be easily calculated without much extra cost. It can provide an evidence basis to support societal debates and decision making processes about biodiversity conservation in forests at large-scale. The expression of structural diversity in a single number allows a direct comparison among different types of forest stands and it facilitates the depiction of changes within single types of forests over time. These are considered important aspects of the reporting on sustainability of forests in a general way. A more specific assessment of individual structural elements used in the index can be easily derived, if the focus is on monitoring particular aspects of structural diversity (e.g. the presence of large living trees or the number of tree species), for example to guide forest management and planning.

Acknowledgements

We like to thank Dr. Gerald Kändler (Forest Research Institute of Baden-Württemberg, Dep. of Biometry and Informatics) for supporting the analyses of NFI data. Also special thanks to Joachim Maack for support with statistical analysis.

This work was supported by a grant from the Ministry of Science, Research and the Arts of Baden-Württemberg (7533-10-5-78) to Jürgen Bauhus. Felix Storch received additional support through the BBW ForWerts Graduate Program.

2.6 References

Abrahamsson M, Lindbladh M (2006) A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (Picea abies). In: Forest Ecology and Management 226 (1-3), S. 230–237. DOI: 10.1016/j.foreco.2006.01.046.

Acker SA, Sabin TE, Ganio LM, McKee WA (1998) Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. In: Forest Ecology and Management 104 (1-3), S. 265–280. DOI: 10.1016/S0378-1127(97)00249-1.

Andrews SP, Gration G, Quin D, Smith AP (1994) Description and assessment of forestry impacts on fauna of the Urbenville Forestry Management Area. Supporting Document, 4.

Bachofen H, Zingg A (2001) Effectiveness of structure improvement thinning on stand structure in subalpine Norway spruce (Picea abies (L.) Karst.) stands. In: Forest Ecology and Management 145 (1-2), S. 137–149. DOI: 10.1016/S0378-1127(00)00581-8.

Barbier S, Chevalier R, Loussot P, Bergès L, Gosselin F (2009) Improving biodiversity indicators of sustainable forest management. Tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. In: Forest Ecology and Management 258, S176-S186. DOI: 10.1016/j.foreco.2009.09.004.

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved— A critical review for temperate and boreal forests. In: Forest Ecology and Management 254 (1), S. 1–15. DOI: 10.1016/j.foreco.2007.09.038.

Barnett JL, How RA, Humphreys WF (1978) The use of habitat components by small mammals in eastern Australia. In: Austral Ecol 3 (3), S. 277–285. DOI: 10.1111/j.1442-9993.1978.tb01177.x.

Bauhus J, Pyttel P (2015) Managed forests. In: Peh KSH, Corlett RT and Bergeron Y (eds.) Routledge Handbook of Forest Ecology. Routledge, Oxon, pp.75-90.

Bauhus J, Puettmann KJ, Kuehne C (2013) Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In: Messier C, Puettmann KJ and Coates KD (eds.): Managing Forests as Complex Adaptive Systems: building resilience to the challenge of global change. Routledge, The Earthscan forest library, pp. 187-213.

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. In: Forest Ecology and Management 258 (4), S. 525–537. DOI: 10.1016/j.foreco.2009.01.053.

Bazzaz FA (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology, 56(2), 485-488.

Bhadra B, Rao RS, Singh PK, Sarkar PK, Shivaji S (2008) Yeasts and yeast-like fungi associated with tree bark: diversity and identification of yeasts producing extracellular endoxylanases. Current microbiology, 56(5), 489-494.

Bitterlich W (1948) Die Winkelzählprobe (The Angle-Count Sample Plot). Allgm. Forst-u. Holzwirtz. Ztg., 59: 4-5. In Forestry Abstracts (Vol. 10, p. 2314).

Blaser S, Prati D, Senn-Irlet B, Fischer M (2013) Effects of forest management on the diversity of deadwood-inhabiting fungi in Central European forests. In: Forest Ecology and Management 304, S. 42–48. DOI: 10.1016/j.foreco.2013.04.043.

Bouget C, Larrieu L, Nusillard B, Parmain G (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodiversity and conservation, 22(9), 2111-2130.

Boyden S, Binkley D, Shepperd W (2005) Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range. In: Forest Ecology and Management 219 (1), S. 43–55. DOI: 10.1016/j.foreco.2005.08.041.

Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. In: J Insect Conserv 15 (5), S. 653–669. DOI: 10.1007/s10841-010-9364-5.

Brunialti G, Frati L, Aleffi M, Marignani M, Rosati L, Burrascano S, Ravera S (2010) Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. In: Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 144 (1), S. 221–233. DOI: 10.1080/11263500903560959.

Bütler R, Lachat T, Larrieu L, Paillet Y (2013) 2.1 Habitat trees: key elements for forest biodiversity. Integrative approaches as an opportunity for the conservation of forest biodiversity, 84.

Burgman MA, Breininger DR, Duncan BW, Ferson S (2001) Setting reliability bounds on habitat suitability indices. In: Ecological Applications 11 (1), S. 70–78

Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests. A global review. In: Forest Ecology and Management 291, S. 458–479. DOI: 10.1016/j.foreco.2012.11.020.

Burrascano S, Sabatini FM, Blasi C (2011) Testing indicators of sustainable forest management on understorey composition and diversity in southern Italy through variation partitioning. In: Plant Ecol 212 (5), S. 829–841. DOI: 10.1007/s11258-010-9866-y.

Burrascano S, Lombardi F, Marchetti M (2008) Old-growth forest structure and deadwood. Are they indicators of plant species composition? A case study from central Italy. In: Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 142 (2), S. 313–323. DOI: 10.1080/11263500802150613.

Castagneri D, Garbarino M, Berretti R, Motta R (2010) Site and stand effects on coarse woody debris in montane mixed forests of Eastern Italian Alps. In: Forest Ecology and Management 260 (9), S. 1592–1598. DOI: 10.1016/j.foreco.2010.08.008.

Chirici G, Winter S, McRoberts RE (2011) National Forest Inventories. Dordrecht: Springer Netherlands (Managing Forest Ecosystems, v.20).

Corona P (2016) Consolidating new paradigms in large-scale monitoring and assessment of forest ecosystems. Environ Res 144:8–14

Corona P, Chirici G, McRoberts RE, Winter S, Barbati A (2011) Contribution of large-scale forest inventories to biodiversity assessment and monitoring. In: Forest Ecology and Management 262 (11), S. 2061–2069. DOI: 10.1016/j.foreco.2011.08.044.

Corona P, Köhl M, Marchetti M (Eds.) (2003) Advances in forest inventory for sustainable forest management and biodiversity monitoring (Vol. 76, pp. 1-441). Dordrecht: Kluwer Academic Publishers.

Denslow JS, Guzman S, (2000) Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. J. Vegetation Sci. 11, 201–212.

Dickman CR (1991) Use of trees by ground-dwelling mammals: implications for management. Conservation of Australia's forest fauna, 125-136.

Dittrich S, Jacob M, Bade C, Leuschner C, Hauck M (2014) The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. In: Plant Ecol 215 (10), S. 1123–1137. DOI: 10.1007/s11258-014-0371-6.

Drapeau P, Nappi A, Imbeau L, Saint-Germain M (2009) Standing deadwood for keystone bird species in the eastern boreal forest. Managing for snag dynamics. In: The Forestry Chronicle 85 (2), S. 227–234. DOI: 10.5558/tfc85227-2.

Du Bus de Warnaffe G, Deconchat M (2008) Impact of four silvicultural systems on birds in the Belgian Ardenne: implications for biodiversity in plantation forests.Biodivers Conserv 17(5):1041–1055. https://doi.org/10.1007/s10531-008-9364-x

Duelli P, Obrist MK (2003) Biodiversity indicators. The choice of values and measures. In: Agriculture, Ecosystems & Environment 98 (1-3), S. 87–98. DOI: 10.1016/S0167-8809(03)00072-0.

Dueser RD, Shugart HH (1978) Microhabitats in a Forest-Floor Small Mammal Fauna. In: Ecology 59 (1), S. 89–98. DOI: 10.2307/1936634.

Eyre TJ, Smith AP (1997) Floristic and structural habitat preferences of yellow-bellied gliders (Petaurus australis) and selective logging impacts in southeast Queensland, Australia. Forest Ecology and Management, 98(3), 281-295.

Ferreira LV, Prance GT (1999) Ecosystem recovery in terra firme forests after cutting and burning. A comparison on species richness, floristic composition and forest structure in the Jaú National Park, Amazonia. In: Botanical Journal of the Linnean Society 130 (2), S. 97–110. DOI: 10.1111/j.1095-8339.1999.tb00514.x.

Gardner TA (2010) Monitoring Forest Biodiversity: Routledge.

Geburek T, Milasowszky N, Frank G, Konrad H, Schadauer K (2010) The Austrian Forest Biodiversity Index. All in one. In: Ecological Indicators 10 (3), S. 753–761. DOI: 10.1016/j.ecolind.2009.10.003.

Gilmore AM (1985) The influence of vegetation structure on the density of insectivorous birds. In: Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management (eds Keast A, Recher HF, Ford HA and Saunders DA), pp. 21–31. Surrey Beatty & Sons, Chipping Norton, NSW.

Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, Lindenmayer D B, Lõhmus A, Martínez Pastur G, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney WJA, Wayne A, Franklin JF (2012) Retention Forestry to Maintain Multifunctional Forests: a World Perspective. Bioscience 62, 7, 633-645

Hao Z, Zhang J, Song B, Ye J, Li B (2007) Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. In: Forest Ecology and Management 252 (1-3), S. 1–11. DOI: 10.1016/j.foreco.2007.06.026.

Hatanaka N, Wright W, Loyn RH, Mac Nally R (2011) 'Ecologically complex carbon'- linking biodiversity values, carbon storage and habitat structure in some austral temperate forests. In: Global Ecology and Biogeography 20 (2), S. 260–271. DOI: 10.1111/j.1466-8238.2010.00591.x.

Hello P (1985) Effects of forest regeneration on the structure of bird communities in northern Finland. In: Ecography 8 (2), S. 120–132. DOI: 10.1111/j.1600-0587.1985.tb01162.x.

Herrera M, Gerardo L, Hobson KA, Manzo AA, Estrada BD, Sánchez-Cordero V, Méndez CG (2001) The Role of Fruits and Insects in the Nutrition of Frugivorous Bats. Evaluating the Use of Stable Isotope Models1. In: Biotrop 33 (3), S. 520. DOI: 10.1646/0006-3606(2001)033[0520:TROFAI]2.0.CO;2.

Hoover CM, Leak WB, Keel BG (2012) Benchmark carbon stocks from old-growth forests in northern New England, USA. In: Forest Ecology and Management 266, S. 108–114. DOI: 10.1016/j.foreco.2011.11.010.

Hoppe B, Purahong W, Wubet T, Kahl T, Bauhus J, Arnstadt T (2016) Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. In: Fungal Diversity 77 (1), S. 367–379. DOI: 10.1007/s13225-015-0341-x.Houghton RA (2005): Aboveground Forest Biomass and the Global Carbon Balance. In: Global Change Biol 11 (6), S. 945–958. DOI: 10.1111/j.1365-2486.2005.00955.x.

Houghton RA (2005) Aboveground forest biomass and the global carbon balance. Global change biology, 11(6), 945-958.

Humphrey JW, Davey S, Peace AJ, Ferris R, Harding K (2002) Lichens and bryophyte communities of planted and semi-natural forests in Britain. The influence of site type, stand structure and deadwood. In: Biological Conservation 107 (2), S. 165–180. DOI: 10.1016/S0006-3207(02)00057-5.

Kändler G, Cullmann D (2014) Der Wald in Baden-Württemberg. Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg (FVA).

Kändler G (2006) Abschlussbericht zum Vorhaben ”Vertiefende Analyse der BWI2-Daten unter den Aspekten Naturnähe und Biodiversität“

Kappes H, Topp W (2004) Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. Biodiversity and Conservation, 13, 1905–1924.

Kavanagh RP (1987) Forest Phenology and Its Effect on Foraging Behavior and Selection of Habitat by the Yellow-Bellied Glider, Petaurus-Australis Shaw. Wildlife Research, 14(4), 371-384.

Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. In: Forest Ecology and Management 235 (1-3), S. 129–142. DOI: 10.1016/j.foreco.2006.08.005.

Koop H, Rijksen HD, Wind J (1995) Tools to diagnose forest integrity; an appraisal method substantiated by SILVI-STAR assessment of diversity and forest structure. In IUFRO Symposium, Chiang Mai (Thailand), 27 Aug-2 Sep 1994. CIFOR.

Kuuluvainen T (2009) Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe. The Complexity Challenge. In: AMBIO: A Journal of the Human Environment 38 (6), S. 309–315. DOI: 10.1579/08-A-490.1.

Lachat T, Bouget C, Bütler R, Müller J (2013) Totholz: Quantitative und qualitative Voraussetzungen für die Erhaltung der biologischen Vielfalt von Xylobionten; see Kraus & Krumm (2013)

Lähde E, Laiho O, Norokorpi Y, Saksa T (1994) Structure and yield of all-sized and even-sized conifer-dominated stands on fertile sites. In: Ann. For. Sci. 51 (2), S. 97–109. DOI: 10.1051/forest:19940201.

Lappi J, Bailey RL (1987) Estimation of the diameter increment function or other tree relations using angle-count samples.

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Canadian Journal of Forest Research, 42(8), 1433-1445.

Larsson TB (2001) Biodiversity evaluation tools for European forests. In: Ecological Bulletins, vol. 50, Wiley-Blackwell, pp. 240., 2001.

Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity. Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. In: Ecological Indicators 11 (5), S. 1027–1039. DOI: 10.1016/j.ecolind.2011.02.004.

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity. A comprehensive multiscaled approach. Washington, DC: Island Press.

Lindenmayer DB, Margules CR, Botkin DB (2000) Indicators of Biodiversity for Ecologically Sustainable Forest Management. In: Conservation Biology 14 (4), S. 941–950. DOI: 10.1046/j.1523-1739.2000.98533.x.

Lombardi F, Cocozza C, Lasserre B, Tognetti R, Marchetti M (2011) Dendrochronological assessment of the time since death of dead wood in an old growth Magellan's beech forest, Navarino Island (Chile). In: Austral Ecology 36 (3), S. 329–340. DOI: 10.1111/j.1442-9993.2010.02154.x.

Lombardi F, Marchetti M, Corona P, Merlini P, Chirici G, Tognetti R, Burrascano S, Alivernini A, Puletti N (2015) Quantifying the effect of sampling plot size on the estimation of structural indicators in old-growth forest stands. Forest Ecol Manag 346:89–97

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology, 42, 594–598.

MacFarlane DW, Luo A (2009): Quantifying tree and forest bark structure with a bark-fissure index. In: Can. J. For. Res. 39 (10), S. 1859–1870. DOI: 10.1139/X09-098.

Maltamo M (1997) Comparing basal area diameter distributions estimated by tree species and for the entire growing stock in a mixed stand.

Margules CR, Pressey RL, Williams PH (2002) Representing biodiversity. Data and procedures for identifying priority areas for conservation. In: J Biosci 27 (4), S. 309–326. DOI: 10.1007/BF02704962.

McElhinny C, Gibbons P, Brack C (2006) An objective and quantitative methodology for constructing an index of stand structural complexity. In: Forest Ecology and Management 235 (1-3), S. 54–71. DOI: 10.1016/j.foreco.2006.07.024.

Meyer P (1999) Totholzuntersuchungen in nordwestdeutschen Naturwäldern. Methodik und erste Ergebnisse. In: Forstw Cbl 118 (1-6), S. 167–180. DOI: 10.1007/BF02768985.

Michel AK, Winter S, Linde A (2011) The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (Pseudotsuga menziesii var. menziesii). In: Can. J. For. Res. 41 (2), S. 300–308. DOI: 10.1139/X10-207.

Mosimann P, Naef-Daenzer B, Blattner M (1987) Die Zusammensetzung der Avifauna in typischen Waldgesellschaften der Schweiz. Der Ornithologische Beobachter, 84, 275-299.

Müller J, Bußler H, Kneib T (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. In: J Insect Conserv 12 (2), S. 107–124. DOI: 10.1007/s10841-006-9065-2.

Neumann M, Starlinger F (2001) The significance of different indices for stand structure and diversity in forests. In: Forest Ecology and Management 145 (1-2), S. 91–106. DOI: 10.1016/S0378-1127(00)00577-6.

Newsome AE, Catling PC (1979) Habitat preferences of mammals inhibiting heathlands of warm temperate coastal, montane and alpine regions of southeastern Australia. In: Specht RL (Ed.), Ecosystems of the World, vol. 9A. Heathlands and Related Shrublands. Descriptive Studies, Elsevier, Amsterdam, pp. 301–316.

Niemeijer D, de Groot RS (2008) Framing environmental indicators: moving from causal chains to causal networks. Environ Dev Sustain 10(1):89–106

Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. In: Forest Ecology and Management 161 (1-3), S. 189–204. DOI: 10.1016/S0378-1127(01)00480-7.

Norris C, Hobson P, Ibisch PL (2011) Microclimate and vegetation function as indicators of forest thermodynamic efficiency. In: Journal of Applied Ecology, no-no. DOI: 10.1111/j.1365-2664.2011.02084.x.

Noss RF (1990) Indicators for Monitoring Biodiversity. A Hierarchical Approach. In: Conservation Biology 4 (4), S. 355–364. DOI: 10.1111/j.1523-1739.1990.tb00309.x.

OECD (2003) OECD environmental indicators: development, measurement and use. Reference paper, Paris, p 50

Okland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation , 76, 297–310.

Parkes D, Newell G, Cheal D (2003) Assessing the quality of native vegetation: the ‘habitat hectares’ approach. Ecological Management & Restoration, 4(s1).

Pearce J (1996) Habitat selection by the white-eared honeyeater. II. A case study at Yellingbo State Nature Reserve, south-east Victoria. Emu-Austral Ornithology, 96(1), 50-54.

Persiani AM, Audisio P, Lunghini D, Maggi O, Granito VM, Biscaccianti AB (2010) Linking taxonomical and functional biodiversity of saproxylic fungi and beetles in broad-leaved forests in southern Italy with varying management histories. In: Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 144 (1), S. 250–261. DOI: 10.1080/11263500903561114.

Pielou EC (1975) Ecological Diversity Wiley & Sons. *New York*.

Plieninger T, Bieling C, Gerdes H, Ohnesorge B, Schaich H, Schleyer C, Wolff F (2010) Ökosystemleistungen in Kulturlandschaften–Konzept und Anwendung am Beispiel der Biosphärenreservate Oberlausitz und Schwäbische Alb. Natur und Landschaft, 85(5), 187-192.

Polley H, Kroiher F (2017) Nadelwälder in Deutschland. In Pro Wald, March 2017, S. 4-7.

Polley H (2010) Monitoring in Wäldern: Die Bundeswaldinventur und Verknüpfungen für Naturschutzfragen. Naturschutzmonitoring in Deutschland. Stand und Perspektiven. Naturschutz und Biologische Vielfalt, 83, 65-78.

Polley H (2005) Die zweite Bundeswaldinventur - BWI^2 - Der Inventurbericht. Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz.

Pretzsch H (2005) Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (Fagus sylvatica L.). Evidence from long-term experimental plots. In: Eur J Forest Res 124 (3), S. 193–205. DOI: 10.1007/s10342-005-0068-4.

Pretzsch H (2003) Diversität und Produktivität von Wäldern. Allgemeine Forst-und Jagdzeitung, 174, 88-98.

Pretzsch H (1997) Analysis and modelling of spatial stand structures. Methodological considerations based on mixed beechlarch stands in Lower Saxony. Forest Ecol. Manage. 97, 237–253.

Raison RJ, Flinn DW, Brown AG (2001) Application of criteria and indicators to support sustainable forest management: some key issues. CAB International, 2001. In: In Criteria and (2001).

Ranius T, Ekvall H, Jonsson M, Bostedt G (2005) Cost-efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. In: Forest Ecology and Management 206 (1-3), S. 119–133. DOI: 10.1016/j.foreco.2004.10.061.

Recher HF (1991) The conservation and management of eucalypt forest birds: resource requirements for nesting and foraging. Conservation of Australia's forest fauna, 25-34.

Ritter T, Saborowski J (2012) Point transect sampling of deadwood. A comparison with well-established sampling techniques for the estimation of volume and carbon storage in managed forests. In: Eur J Forest Res 131 (6), S. 1845–1856. DOI: 10.1007/s10342-012-0637-2.

Rondeux J, Sanchez C (2010) Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable. Deadwood. In: Environmental monitoring and assessment 164 (1-4), S. 617–630. DOI: 10.1007/s10661-009-0917-6.

Sabatini FM, Burrascano S, Lombardi F, Chirici G, Blasi C (2015) An index of structural complexity for Apennine beech forests. In: iForest 8 (3), S. 314–323. DOI: 10.3832/ifor1160-008.

Scherzinger W(1996) Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung. Praktischer Naturschutz.—Stuttgart (Verlag Eugen Ulmer).—447 S., 51 Farbabb., 119 s/w-Abb., 36 Tab. ISBN 3-8001-3356-3. Zoosystematics and Evolution, 74(1), 149-149.

Simpson EH (1949) Measurement of diversity. Nature, 163, 688.

Singh KP, Kushwaha CP (2005) Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. Annals of Botany, 97(2), 265-276.

Smith AP, Andrews SP, Moore DM (1994) Terrestrial Fauna of the Grafton and Casino State Forest Management Areas: Description and assessment of impacts. Grafton EIS.

Soderquist TR, MacNally R (2000) The conservation value of mesic gullies in dry forest landscapes: mammal populations in the box–ironbark ecosystem of southern Australia. Biological Conservation, 93(3), 281-291.

Spies TA, Franklin JF (1991) The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-285, Portland, USA. Pacific Northwest Research Station, 91-111.

Staudhammer CL, LeMay VM (2001) Introduction and evaluation of possible indices of stand structural diversity. In: Can. J. For. Res. 31 (7), S. 1105–1115. DOI: 10.1139/cjfr-31-7-1105.

Sterba H (2008) Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. In: Forestry 81 (5), S. 587–597. DOI: 10.1093/forestry/cpn010.

Sullivan TP, Sullivan DS, Lindgren PMF (2001) Stand Structure and Small Mammals in Young Lodgepole Pine Forest. 10-Year Results after Thinning. In: Ecological Applications 11 (4), S. 1151. DOI: 10.2307/3061019.

Taboada Á, Tárrega R, Calvo L, Marcos E, Marcos JA, Salgado JM (2010) Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. In: Eur J Forest Res 129 (1), S. 31–45. DOI: 10.1007/s10342-008-0245-3.

Tanabe S, Toda MJ, Vinokurova AV (2001) Tree shape, forest structure and diversity of drosophilid community. Comparison between boreal and temperate birch forests. In: Ecol Res 16 (3), S. 369–385. DOI: 10.1046/j.1440-1703.2001.00402.x.

Tilman D (1999) The ecological consequences of changes in. A search for general principles 101. In: Ecology 80 (5), S. 1455–1474. DOI: 10.1890/0012-9658(1999)080

Tomppo E, Gschwantner T, Lawrence M, McRoberts RE, Gabler K, Schadauer K, Cienciala E (2010) National forest inventories. Pathways for Common Reporting. European Science Foundation, 541-553.

Tyrrell LE, Crow TR (1994) Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. In: Ecology 75 (2), S. 370–386. DOI: 10.2307/1939541.

Uuttera J, Tokola T, Maltamo M (2000) Differences in the structure of primary and managed forests in East Kalimantan, Indonesia. In: Forest Ecology and Management 129 (1-3), S. 63–74. DOI: 10.1016/S0378-1127(99)00157-7.

Uuttera J, Maltamo M, Hotanen JP (1997) The structure of forest stands in virgin and managed peatlands. A comparison between Finnish and Russian Karelia. In: Forest Ecology and Management 96 (1-2), S. 125–138. DOI: 10.1016/S0378-1127(97)00035-2.

Van den Meersschaut D, Vandekerkhove K (2000) Development of a stand-scale forest biodiversity index based on the State Forest Inventory.

Verkerk PJ, Lindner M, Zanchi G, Zudin S (2011) Assessing impacts of intensified biomass removal on deadwood in European forests. In: Ecological Indicators 11 (1), S. 27–35. DOI: 10.1016/j.ecolind.2009.04.004.

Watson J, Freudenberger D, Paull D (2001) An Assessment of the Focal-Species Approach for Conserving Birds in Variegated Landscapes in Southeastern Australia. In: Conservation Biology 15 (5), S. 1364–1373. DOI: 10.1111/j.1523-1739.2001.00166.x.

Whitman AA, Hagan JM (2007) An index to identify late-successional forest in temperate and boreal zones. In: Forest Ecology and Management 246 (2-3), S. 144–154. DOI: 10.1016/j.foreco.2007.03.004.

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. In: Forest Ecology and Management 255 (3-4), S. 1251–1261. DOI: 10.1016/j.foreco.2007.10.029.

Woinarski JCZ, Recher HF, Majer JD (1997) Vertebrates of eucalypt formations. In ‘Eucalypt Ecology: Individuals to Ecosystems’.(Eds Williams JE and Woinarski JCZ.) pp. 303–341.

Ziegler SS (2000) A comparison of structural characteristics between old-growth and postfire second-growth hemlock-hardwood forests in Adirondack Park, New York, U. S. A. In: Global Ecol Biogeography 9 (5), S. 373–389. DOI: 10.1046/j.1365-2699.2000.00191.x.

Zotti M, Persiani AM, Ambrosio E, Vizzini A, Venturella G, Donnini, D (2013) Macrofungi as ecosystem resources. Conservation versus exploitation. In: Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 147 (1), S. 219–225. DOI: 10.1080/11263504.2012.753133.

Chapter 3: Linking structural- to species-diversity of forests: An index-based approach

Examples of taxonomic groups:

a) *Carabus problematicus*, TG: coleoptera (*), b) purple foxglove (*Digitalis purpurea*), TG: vascular plants (*), c) Eurasian jay (*Garrulus glandarius*), TG: birds (*), d), lichen and moss, TGs: lichen and bryophytes e) fly agaric (*Amantia muscaria*), TG: fungi (*), f) red wood ant (*Formica rufa*), TG: formicidae (*)

a)

b)

c)

d)

e)

f)

(*): pictures taken by Felix Storch

Linking structural diversity to species-diversity of forests: An index-based approach

Felix Storch[1], Carsten F. Dormann[2], Marco Tschapka[3], Martin M. Gossner[4], Markus Fischer[5], Heike Feldhaar[6], Rolf Daniel[7], Tesfaye Wubet[8], Andrea Polle[9], Christian Ammer[10], Peter Schall[10], Wolfgang Weisser[11] and Jürgen Bauhus[1]

[1] Chair of Silviculture, Albert-Ludwigs-University of Freiburg, Germany
[2] Chair of Biometry, Albert-Ludwigs-University of Freiburg, Germany
[3] Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Germany
[4] Forest Entomology, Swiss Federal Research Institute WSL, Switzerland
[5] Institute of Plant Sciences, University of Bern, Switzerland
[6] Faculty of Biology, Chemistry & Earth Sciences, University of Bayreuth, Germany
[7] Institute of Microbiology and Genetics, Georg-August-University of Göttingen, Germany
[8] Ecosystems of the Future, Soil Ecology, Helmholtz Centre for Environmental Research, Halle, Germany
[9] Forest Botany and Tree Physiology, Georg-August-University of Göttingen, Germany
[10] Silviculture and Forest Ecology, Georg-August-University of Göttingen, Germany
[11] Chair for Terrestrial Ecology, Technical University of Munich, Germany

Author for correspondence

Felix Storch

Tel: +49-(0)761-203-8628

Fax: +49-(0)761-203-3781

Email: *felix.storch@waldbau.uni-freiburg.de*

Key words: *structural diversity, species diversity, structural diversity index, biodiversity monitoring, large-scale inventory*

Type of paper: synthesis paper

3.1 Abstract

Owing to the difficulties of monitoring diversity of forest dwelling species directly, forest structure has been suggested to be used as a surrogate that is more easy to monitor, for example in broad scale inventories. Here we wanted to investigate, whether an index of stand structural diversity (FSI), which had been developed from forest attributes of the German National Forest Inventory, could be calibrated against the diversity means species richness and diversity of a wide range of taxonomic groups.

For that purpose, we used information on forest structure and species richness of a broad range of taxonomic groups that had been determined for 150 forest plots of the German Biodiversity Exploratories that cover a range in management intensities. We then tested whether the forest structure index calculated for these forest plots can predict diversity means species richness of these taxonomic groups, assuming that the structural attributes captured by the index represent the habitat requirements of the species.

Correlations between the FSI and diversity means richness of species within individual TGs were analysed at the plot-level. The strength of relationships between the structural diversity index and species richness of TGs was highly variable. For some groups such as birds or deadwood fungi, it was possible to describe the diversity means species richness in some regions and for some types of forests. Diversity means species richness of other TGs such as bats or harvestmen could not be described by the FSI. In these cases, positive correlations between species richness and individual structural attributes of the index were cancelled out by negative correlations with other structural attributes. The diversity means species richness in other taxonomic groups was neither captured by the index nor by individual structural attributes contained in the index, indicating that further variables determine habitat quality for species of these TGs.

Results of this study show the general possibility to use variables of forest structure to predict diversity means species richness of different taxonomic groups, albeit not of all taxonomic groups. This information may be useful to support biodiversity monitoring through quantification of forest structure in large-scale forest inventories.

3.2 Introduction

As biodiversity is lost at an increasing rate (e.g. BMU 2011, Lindenmayer & Franklin 2002), the protection of ecosystems and biodiversity becomes more important in political and economic decision making processes. Yet in many jurisdictions, public-forest authorities are requested to monitor biodiversity and report on their management efforts to maintain or improve biodiversity (e.g. FFH-areas). However biodiversity or species-diversity is extremely difficult and very expensive to monitor (Gardner 2010, Lindenmayer & Franklin 2002). This is caused, for example, by taxon-specific characteristics such as large home-ranges, seasonal appearances or expensive sampling efforts. In addition, there is no established or widely accepted approach to monitor biodiversity across many sites (Noss 1990, Pielou 1975). Therefore, a supporting way would be helpful, provided by information about structural diversity of forests as a surrogate for habitat quality for different taxonomic groups (Gardner 2010, Lindenmayer & Franklin 2002).

Forest management activities can lead to changes in stand structure or habitat availability and quality and consequently to changes in species diversity (Kuuluvainen 2009, Raison *et al.* 2001, Lindenmayer *et al.* 2000). Practical conservation management typically means extending rotation periods, excluding trees with microhabitats from harvests, increasing deadwood volume in forests or even creating standing dead trees and high stumps artificially (Bauhus *et al.* 2009, Abrahamsson & Lindbladh 2006, Ranius *et al.* 2005). However, so far the evaluation of effects of management on stand structure and biodiversity has been largely confined to case studies or to particular taxonomic groups. Larrieu *et al.* (2018) analysed the sampling methods of different microhabitats across many Mediterranean forest sites. But often these were simple comparisons between managed and unmanaged forests without consideration of different harvesting intensities (e.g. Paillet *el al.* 2010.). However, recent studies like Schall *et al.* (2018) compared influences of forest management on structure and biodiversity across different stands and thereby on a larger-scale. While we have an extensive spatial coverage of information about forest structure and harvesting intensity through large-scale forest inventories, quantitative and comprehensive assessments of biodiversity have been carried out at few places only.

To analyse relationships between structural-diversity and species-diversity, data of three regions in Germany were used in our study, which was conducted within the DFG cooperative project '*German Biodiversity Exploratories*' (*GBE,* Map 3.1; Fischer *et al.* 2010): Swabian Alb (Baden-Württemberg), Hainich (Thuringia) and Schorfheide (Brandenburg). For 50 plots of 1 ha in size at each of these exploratories not only variables of forest structure but also the presence or absence of species in a wide range of taxonomic groups has been analysed (references). In addition, these plots represent a gradient of forest management intensity within each exploratory (e.g. Kahl and Bauhus 2014).

In forest ecology, the 'habitat heterogeneity hypothesis' and the 'more-individuals hypothesis' are general and accepted assumptions (e.g. Müller *et al.* 2018, MacArthur & Wilson 1967, Simpson 1949). It assumes that structurally diverse forests provide more niches and habitats and thereby harbour a higher species diversity than structurally poor stands (Jung *et al.* 2012, Taboada *et al.* 2010, Bazzaz 1975). In most forest ecosystems, plant communities influence structural diversity and have a considerable impact on species diversity (e.g. McCoy & Bell, 1991). MacArthur & MacArthur (1961) showed for example, that diversity of birds can be influenced more strongly by vertical heterogeneity of forest stands than by composition of tree species. These relationships have been well analysed for some TGs at the local and regional level (Davidowitz & Rosenzweig 1998; Schall *et al.* 2018), but not across different types of forest ecosystems. In addition, higher structural diversity at the plot level or the stand level can lead to a reduction in species diversity (e.g. Sullivan & Sullivan 2001, Ralph 1985), because positive effects of structural elements for one taxonomic group can be negative for other taxonomic groups, which has to be kept in mind when analysing diversity for different taxonomic groups or the overall diversity of species, comprehensively (Schall *et al.* 2018, Okland 1996).

In this study, we investigated how well stand structural diversity correlates with species richness of a wide range of taxonomic groups at intensively studied sites in three regions of Germany. This information might be used for indirect biodiversity monitoring through large scale forest inventories containing that permit a comprehensive quantification of forest structural attributes.

3.3 Material & Methods

3.3.1 Study sites

Figure 3.1. German Biodiversity Exploratories located in three regions of Germany: Swabian Alb (Baden-Württemberg), Hainich (Thuringia) and Schorfheide (Brandenburg)

This study was carried out with data on forest structure and the species richness of a wide range of taxonomic groups that were collected in 150 forest plots from three regions of the German Biodiversity Exploratories (GBE) (Swabian Alb, Baden-Württemberg, Hainich, Thuringia and Schorfheide, Brandenburg; see Fischer *et al.* 2010 and Figure 3.1). The plots are located in forest stands dominated by European beech (*Fagus sylvatica*) (managed and unmanaged), oak-dominated stands (*Qercus robur* and *Quercus petraea*), and stands dominated by Norway spruce (*Picea abies*) and Scotspine (*Pinus sylvestris*) as well as different stand development phases (thicket, pole-stage, immature and mature). In each of these regions there are 50 plots of 1 ha in size that span a gradient in forest management intensity from intensively managed to un-managed stands. On these plots, experts sampled and analysed the species richness of a wide range of taxonomic groups. Further information about the German Biodiversity Exploratories can be found in Fischer *et al.* (2010) and at: <http://www.biodiversity-exploratories.de/1/home>. An overview of sampled taxonomic groups that were used in this analysis as well as owner of data-sets and IDs of data-sets are summarized in Table 3.1.

Table 3.1. Overview of applied data-sets and IDs of the German Biodiversity Exploratories to assess the performance of the FSI referred to different TGs; *: set of data-sets

Taxonomic Group	Dataset-ID	Taxonomic Group	Dataset-ID
Bats	19849, 19850, 19851, 19852	Soil Fungi	21047
Birds	21446, 21447, 21448, 21449, 21450	Mycorrhiza Fungi	19186
Small mammals	3901, 5840	Hymenoptera	16906
Arthropods*	set of data-sets	Araneae	16868
Coleoptera	16866	Plants	6240
Bark Beetle antagonists	20034	Number Vascular Plants	6240, 14410
Formicidae	not from Bexis	Forest inventory	18268, 21426
Lichen	4460	Hemiptera	16867
Bryophytes	4141	Opiliones	16887
Bacteria	19526	Neuroptera	16869
Number Herbs	6240, 14410	Orthoptera	16886
Number Shrubs	6240, 14410	Species Richness sum*	set of data-sets
Deadwood Fungi	17186, 18547		

We selected and tested these taxonomic groups to cover a range of different responses to structural elements of forests. As shown in Table 3.1, a broad selection of taxonomic groups was applied in our study to focus not on rare or endangered species (often referred to structure of old-growth stands; e.g. the taxonomic groups of bats) but on many taxonomic groups that are important for healthy ecosystems (e.g. formicidae). Forest structure was sampled on the same plots of 1 hectare in size, including different sampling techniques like a complete inventory on living trees and deadwood sampling on representative areas to produce reliable results; also see Schall *et al.* (2018) for further information on data on these stands.

3.3.2 Structural diversity index (FSI)

For the purpose of this study we used an index of structural diversity that was developed with data from the National Forest Inventory of Germany (chapter 2). It can be calculated for every sampling point of the national forest inventory and also be easily modified to fit other, similar forest inventories. The use of this index, if it correlates well with other metrics of diversity of forest dwelling species, could permit the prediction of some aspects of forest biodiversity at the scale of the forest inventory. The index comprises 11 variables of forest structure were used to describe 11 different aspects of structural diversity (Table 3.2).

Table 3.2. Variables of forest structure, which are used in the forest structure index, and the aspects of forest structure they represent

Variable	Acronym	Aspect
Quadratic mean diameter at breast height	DBHq	Growing stock
DBH, standard deviation	DBH sd	Uneven-agedness
Volume / ha of trees > 40cm DBH	Vol40	Occurrence of large living trees
Height, standard deviation	Height sd	Vertical heterogeneity
Downed deadwood, mean diameter**	DW d	Deadwood downed
Standing Deadwood mean DBH**	DW s	Deadwood standing
Number of decay classes	N DC	Deadwood decay classes
Species richness of tree regeneration	SR Reg	Regeneration
Tree species richness	SR	Compositional heterogeneity
Bark-diversity*	Bark-diversity	Bark-diversity
Diversity of flowering and fruiting trees* (named as Flower-diversity)	Flower-diversity	Food / pollen diversity

*: calculated as shown in chapter 2; **: threshold value of 20 cm applied to allow comparison to NFI_{2002} data of Germany and transformation of knowledge gained in this analysis

To integrate the information from each variable into the index, the calculated values of each variable had to be transformed into scores. For that purpose, ranges of variables were used and calculated with the formula:

$$X\text{-score} = \frac{(X - X_{min})}{(X_{max} - X_{min})}$$

'X' is the observed value of a variable at the plot-level, with $X_{\min}$ and $X_{\max}$ its extreme values derived from the literature (chapter 2). This leads to variable-scores between 0 (lowest level of SD) and 1 (highest level of SD). To exclude implausible measurements, scores higher than 1 were set to 1. Weightings of individual variables were tested but rejected because a) for a description of the overall structural diversity, no a priori generalizable reason why to favour one or the other measure were present and b) the developed index was robust against weightings between 0 and 2 for individual variables (chapter 2). Finally, these eleven variable-scores were combined in an additive way and divided by the number of variables included (11), which resulted in an overall index-value (also between 0 and 1; see chapter 2 and Table 3.3).

Table 3.3. Equations and examples to calculate the structural diversity index (FSI) at the plot level for forest stands in the German Biodiversity Exploratories; some boundary values (X_{min} and X_{max}) had to be adapted relative to the original (chapter 2) in response to the differences in inventory methods between the Biodiversity Exploratories and the National Forest Inventory.

Aspect	**Variable**	**Equation**	**Fictional Example Score**
Growing stock	DBHq	Score = (X - 9) / (80 - 9)	0.38
Uneven-agedness	DBH sd	Score = (X - 0) / (70 - 0)	0.4
Occurrence of large living trees	Vol40	Score = (X – 0) / (800 - 0)	0.21
Vertical heterogeneity	Height sd	Score = (X - 2) / (25 - 2)	0.5
Deadwood downed	DW d mDM	Score = (X - 0) / (80 - 0)	0.36
Deadwood standing	DW st mDBH	Score = (X - 0) / (80 - 0)	0
Deadwood decay classes	N DC*	Score = (X - 0) / (4 - 0)	0.5
Regeneration	SR Reg	Score = (X - 0) / (8 - 0)	0.18
Compositional heterogeneity	SR	Score = (X - 1) / (16 - 1)	0.22
Bark diversity	Bark-div.	Score = (X - 1) / (26 - 1)	0.25
Food/pollen availability	Flower-div.	Score = (X - 1) / (15 - 1)	0.3
		Sum	3.3
		FSI =3.3 / 11	**= 0.3**

* = the number of decay classes was reduced from 5 to 4 to make it comparable it to NFI-data (the first decay class ‘fresh died’ was removed)

3.3.3 Data preparation of different taxonomic groups

For all analysed taxonomic groups, diversity means species richness was calculated at the plot level. For aggregated sets of groups (for example ‘arthropods’ or ‘sum of species’), data-sets were combined and evaluated also at the plot-level. An overview is provided in supporting information II of chapter 3. Ranges of the diversity of individual TGs for all 150 plots are provided in supporting information VIII of chapter 3.

3.3.4 Data analysis in R

To calculate correlations between diversity means species richness of different taxonomic groups and the forest structure index at the plot level, *cor.test*-function from the R-package *'stats'* was used. These plots were aggregated in types of forests or stand development phases. To focus on reliable correlations, a p-value < 0.1 was used, which is more appropriate for ecological analysis. Significant correlations ≥ 0.3 were considered as robust within ecological analysis and therefore applied in this evaluation. Additionally, to classify as robust correlations should appear over several types of forests or regions.

3.4. Results

3.4.1Variation in forest structural diversity

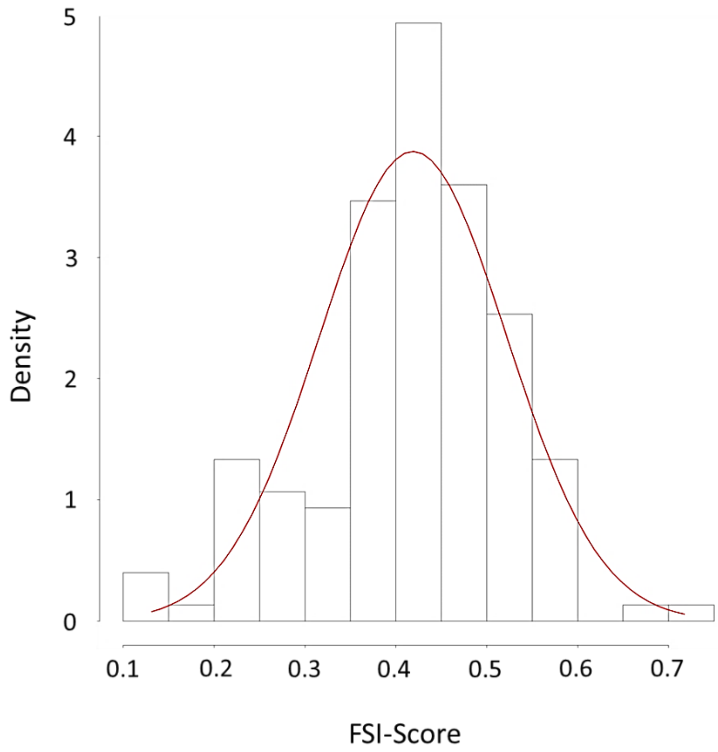


Figure 3.2. Density distribution of the Forest Structure Index (FSI) across 150 sampling plots of 1ha size of the Biodiversity Exploratories; red curve indicates a normal distribution.

The distribution of index-scores at the plot level showed a broad range from structurally poor to structurally diverse forest stands across the forest plots of the Biodiversity Exploratories (Figure 3.2). The left-skewed distribution indicates a dominance of structurally rich ecosystems. At the level of forest types, the highest FSI-score occurred in 'unmanaged mature beech-dominated stands' (0.4) and the lowest FSI-score (0.24) in the young stand development phase ('pole' and 'thicket' are combined to increase the number of inventory plots). Detailed distributions of the Forest Structure Index for separate regions and types of forests can be found in the supporting information III and index-means for all analysed forest strata are provided in supporting information IV of chapter 3.

3.4.2 Relationships between structural diversity and species richness of different taxonomic groups

Results show a heterogeneous picture for the relationship between forest structural diversity and the species richness of different taxonomic groups (supporting information V of chapter 3). Species richness of some taxonomic groups such as birds, deadwood fungi or shrubs could be reasonably well described by the diversity index over most analysed types of forests (correlation coefficient 0.9; cor ≥ 0.3) (Fig. 3.3 and 3.4).

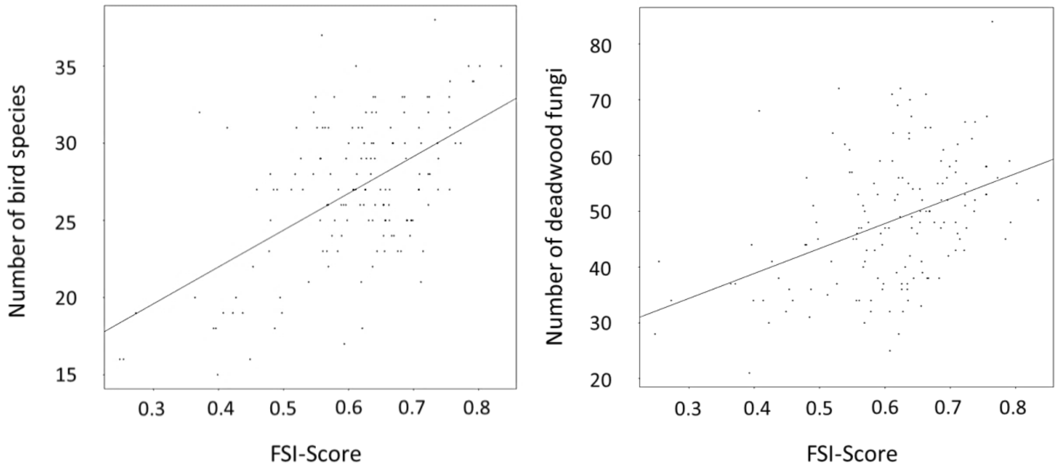


Figure 3.3. Examples for correlations between structural diversity and species richness in the case of birds (left; cor: 0.54, R: 0.29) and deadwood fungi (right; cor: 0.38, R: 0.15) for all sampled plots (N = 150) of the German Biodiversity Exploratories.

The species richness of a second class of taxonomic groups was adequately described by the FSI in only few types of forests or in single regions: for example for hemipteran or formicidae (supporting information V of chapter 3).

The variation in species richness of a third class of TGs such as small mammals, coleoptera was not captured by the FSI at all. The same applies to the total species richness across all studies taxonomic groups (Figure 3.4).

a)

Negative correlated	Positive correlated
Bats (-0.38) Mycorrhiza fungi (-0.39) Araneae (-0.38)	Bacteria (0.46) Birds (0.57) Deadwood fungi (0.5) Plants (0.59) Number vascular plants (0.59) Number of shrubs (0.52) Number of herbs (0.58) Sum of species (0.37) Opiliones (0.52)
Not correlated (correlation with less than two variables)	**Not correlated (variables cancel each other out)**
Arthropods Bryophytes Small mammals Bark Beetles Bark beetle antagonists Orthoptera Coleoptera Hemiptera Formicidae Hymenoptera	Fungi soil Lichen Neuroptera Sum of taxa

b)

Negative correlated	Positive correlated
Bats (-0.49)	Bacteria (0.38) Birds (0.46) Deadwood fungi (0.33)
Not correlated (correlation with less than two variables)	**Not correlated (variables cancel each other out)**
Bryophytes Small mammals Plants Number of herbs Orthoptera Neuroptera Hymenoptera	Arthropods Lichen Mycorrhiza fungi Number vasc. plants Number shrubs Soil fungi Bark beetles Bark beetle antagonists Coleoptera Opiliones Hemiptera Araneae Formicidae Sum of taxa Sum of species

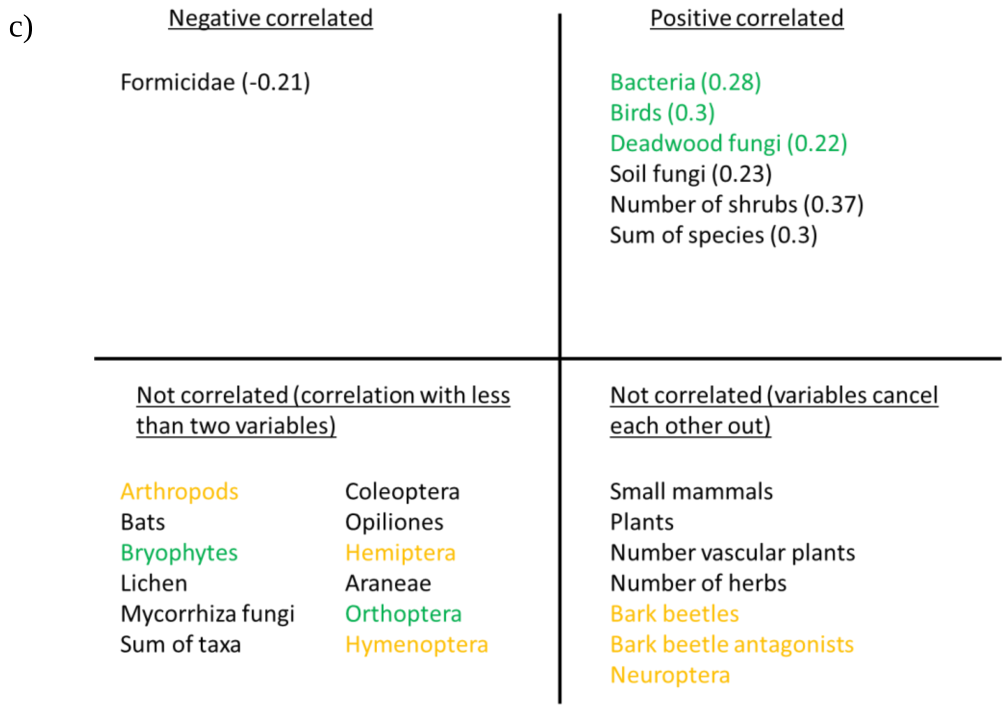


Figure 3.4. Overview of correlations between FSI-score and species richness of taxonomic groups for three different stand development phases (a) 'pole and thicket', b) 'immature' and c) 'mature'); positively, negatively, and not correlated (≤ two variables correlated) and not correlated (variables cancel each other out); number = correlation coefficient within a p-value < 0.1; green: same relationship between FSI und species richness of the taxonomic group across all three developmental stages, orange: same relationship between FSI und species richness of the taxonomic group in two developmental stages.

A complete overview for all analysed types of forests is provided in the supporting information V of chapter 3. To assess, whether species richness of the different taxonomic groups was influenced by particular structural attributes, correlations between species richness of the TGs and individual variables of the FSI were calculated (Table 3.4 and supporting information VI of chapter 3).

Table 3.4. Overview of correlation coefficients for relationships among species richness of selected taxonomic groups and individual variables of the structural diversity index for all plots of the German Biodiversity Exploratories (N = 150); empty fields = no sig. correlation, correlations coefficient 0.9

Taxonomic Group	DBHq	DBH sd	Height sd	SR Reg	SR	Bark-Div	Flower-Div	Vol 40	DW d	DW s	N DC
Arthropods	0.29				-0.14						
Bacteria		0.17	0.2	0.26					0.24	0.18	0.26
Bats	0.38	0.19		-0.23	-0.25	-0.28	-0.19				
Birds	0.43	0.55	0.45				0.17	0.39	0.54	0.33	0.44
Bryophytes		-0.14		0.22							
Deadwood fungi	0.19	0.45	0.49						0.39	0.36	0.36
Soil fungi	-0.18	-0.16		0.15		0.18					
Lichen				0.14							
Small mammals	-0.17	-0.18	-0.14	0.14				-0.24			
Mycorrhiza	0.24				-0.19	-0.16	-0.14	0.15			
Plants	-0.23	-0.25		0.29	0.18	0.22		-0.19			
Vascular plants	-0.25	-0.27		0.28	0.18	0.22		-0.24			
Shrubs	-0.36	-0.27	-0.16	0.44	0.31	0.39	0.23	-0.3			
Herbs	-0.22	-0.25		0.23		0.17		-0.21			
Bark beetles			-0.17			0.16					
Bark beetle antagonists			-0.15				0.17	0.14	-0-16		
Sum of species		0.18	0.17	0.36				0.16	0.22		0.18
Orthoptera											
Colepotera	0.34				-0.15	-0.14					
Opiliones	-0.23	-0.22			0.26	0.26	0.17	-0.25			
Neuroptera			0.21								
Hemiptera	0.26										
Hymenoptera								0.16			
Araneae		-0.28	-0.24					-0.22		-0.14	
Formicidae		-0.19	-0.22	-0.14				-0.25	-0.17		

By analysing these relationships (Table 3.4) for different types of forests of the exploratories, a more reliable statement will be the result if single taxonomic groups can be described by the same variables over different regions or types of forests. An example for the TG of birds is shown in Table 3.5. The variation in species richness of this group is described by the index over different types of forests and stand development phases reasonably well. Besides the variables 'SR Reg', 'SR', 'Bark-diversity' and 'Flower-diversity', all variables in the FSI, as well as the overall FSI-scores, are positive correlated with the group of birds.

Table 3.5. Correlations of individual variables used to calculate the FSI and the taxonomic group of birds for all regions and types of forests of the exploratories (150 plots); empty fields = no sig. correlation, numbers = correlation coefficient, p-value < 0.1; taken from supporting information VI of chapter 3

TG of birds

	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div.	Flower Div.	Vol 40	DW d	DW s	N DC
All plots	0.59	0.43	0.55	0.45				0.17	0.39	0.54	0.33	0.44
Hainich	0.41	0.26	0.25		0.24				0.24	0.36		0.3
Swabian Alb	0.54	0.36	0.63	0.55					0.35	0.5	0.47	0.38
Schorfheide	0.82	0.53	0.6	0.54		0.4	0.3	0.5	0.4	0.78	0.49	0.69
BL-dom.	0.47	0.39	0.58	0.42					0.33	0.47	0.27	0.29
CF-dom.	0.75	0.61	0.64	0.57		0.45	0.49	0.55	0.47	0.64	0.45	0.69
Mature	0.29		0.28			0.21	0.2	0.25		0.23		
Immature	0.49	0.42	0.3						0.34	0.47		0.55
Pole + thicket	0.67	0.57	0.63	0.62					0.59	0.76	0.59	0.6

For all plots within the German Biodiversity Exploratories, species richness can be described by the structural diversity index for 27%[1] of all analysed taxonomic groups.

The correlation between the structural diversity index and species richness across all TGs in mature stands (33%[1] of TGs) was higher than in in immature stands (13%[1]) but lower than in the group of stands in the thicket and pole stage (40%[1] of all tested TGs). These percentages of TGs are even higher, if the focus is only on 'essential' variables for individual TGs and the tendency of correlation (e.g. positive and negative correlated variables might cancel each other so the overall index-values seem not to be significant for the assessment of taxonomic groups). 17%[1] of tested TGs in coniferous-dominated stands and 23%[1] in broadleaf-dominated stands could be described by the FSI; for the region 'Swabian Alb' 37%[1], 'Hainich' 30%[1] and

[1] Number of correlations with a correlation coefficient of 0.9 for all analysed plots of the German Biodiversity Exploratories, divided by the number of possible correlations for a region or forest type

'Schorfheide' 27%[1]. Tables for different types of forests or regions are deposited in supporting information V and VI of chapter 3.

3.5 Discussion
3.5.1 Performance of the FSI

The relatively high average value of the structural diversity index for the GBE (0.32), compared to the average value of all national forest inventory plots of Baden-Württemberg (0.21, NFI_{2012}) may be partially explained by differences in the definition of forest area between forest plots in the Biodiversity Exploratories and the national forest inventory as well as by effects of inventory and sampling design on certain structural variables. Within the GBE, only stocked forest plots are sampled, whereas NFI-plots can be located at forest edges, small tree lines along small creeks (< 5 m width), in regeneration or unstocked forest plots (e.g. if deadwood is present). Including such plots with presumably low structural diversity lowers the average FSI compared to 'real' forest stands. Additionally, inventories of forest plots in the GBE are based on a complete census of all trees with a DBH ≥ 7 cm within plots of 1 ha size, whereas trees of this dimension are sampled in the NFI by angle count sampling. At the plot-level, the average numbers of sampled trees differ greatly between these two sampling methods: 933.4 trees / plot in the full census of the Biodiversity Exploratories, and 7.4 trees / plot or less based on angle count sampling as done in the NFI for Baden-Württemberg; this represents only less than 0.8 % of the complete census individuals). These differences lead to different index-values, assuming that the GBE-inventory produces more exact values than the angle count sampling of NFI, especially when the focus is on rare forest types (strata including only few sampling plots; see chapter 2). For example, conifer-dominated mature stands of the GBE are only represented by 15 plots but analysis is still possible because of many sampled individual trees within a plot, whereas is this stratum was represented by 15 NFI-plots, owing to the method of angle count sampling there would be a much small number of sampled trees (selective sampling; probability proportional to size – see chapter 2, Bitterlich 1948) and hence the measured variables may not be representative. For strata that are represented by many plots, however, a result comparable to complete inventories can be achieved (Sterba 2008, Lappi & Bailey 1987). The extrapolation of information on the relationship between structural diversity and species richness from the GBE to plots of the NFI should be handled carefully, because it would not make sense to predict species richness of different taxonomic groups at the individual NFI plot. This could only be done for matching or similar strata in the NFI. Therefore, the general applicability of the information gained in this analysis to sampling plots of the National Forest Inventory has to be tested in further research because of the representative of individual NFI plots as well as different sampling methods, which might limit the potential for extrapolation to a large scale. Likewise there were differences in measurement protocols of certain structural attributes. For example, to compare deadwood volumes, it was necessary to adapt threshold-values for sampled deadwood. Within the NFI_{2002}, downed deadwood was sampled if the small end diameter is ≥ 20 cm, whereas in the GBE, a threshold-value of 10 cm was applied. By excluding deadwood pieces < 20 cm diameter from the analysis, information on habitat attributes of species depending on small diameter deadwood might get lost. To calculate the FSI-score for inventories using fixed radius circles or complete inventories, it is necessary to adapt threshold values of applied variables (Table 3.3), because values of some variables increase with plot size (e.g. 'SR' or 'Bark-diversity'; see for example Tjørve 2003, Lomolino 2000, Schoener 1976). Therefore, it is important to analyse the inventory data for minimum- and maximum-values of the applied index variables to capture the existing variable-ranges. This adaption is also necessary when applying the FSI to forest ecosystems including different variable ranges like the amount of standing or downed deadwood or the threshold value for large living trees as a surrogate for habitat-tree characteristics.

3.5.2 Relationships between forest structure and species richness

In this analysis, robust correlations with the overall FSI-score were only found for some of the tested taxonomic groups. Variation in species richness of birds or deadwood fungi, for example, appeared to be captured adequately by the FSI. The same direction of this relationship (positive correlation between index-values and diversity of birds / deadwood fungi) was found for different types of forests, as well as for the different geographical regions and all regions pooled, indicating that the pattern is robust (Table 3.4 and supporting information VI of chapter 3). For these types of correlations, it may be worth testing the extrapolation to predict diversity means species richness of birds or deadwood fungi for strata of forest types in the national forest inventory. The correlations between the overall FSI-score and species richness of individual TGs maybe not significant because variables might cancel each other out (positive and negative correlations; for example, species richness of bats over all plots of the GBE was positively correlated with the variables 'DBHq' and 'DBH_sd' and negatively correlated with 'SR', 'SR Reg', 'Bark-diversity' and 'Flower-diversity'; Table 3).

Hence it appears sensible to analyse the relationships between species richness of TG and structure also at the level of individual structural variables of the FSI. An overview about correlations of all analysed taxonomic groups in all regions / types of forests and the FSI is provided in the supporting information VI of chapter 3. By sorting the analysed TGs, important variables can be identified easily (if positive / negative correlations appear in several types of forest stands). These cases are considered as robust and may / can be applied for taxon-specific indices.

In more general terms, the relationships between the variation in certain structural attributes and species richness in different taxonomic groups are supported by previous studies. Zarnowitz & Manuwal (1985) and Mannan & Meslow (1984), for example, showed the importance of large trees, which may also indicate the presence of tree-cavities, for the diversity of birds. The significance of the vertical heterogeneity of vegetation or foliage layers for the diversity of birds, as well as the relative lack of importance of tree species composition, was also found by MacArthur & MacArthur (1961). Also, deadwood-dimensions and decay classes were important structural elements influencing the diversity of forest birds (Mollet *et al.* 2009, Utschick 1991), which corresponds with results of our study. In addition, the importance of standing deadwood as a source of food was shown for woodpeckers by Drapeau *et al.* (2009) and Bütler & Schlaepfer (2004). These ‘old growth’ attributes were also described as important for diversity of birds by Moning & Müller (2008), Laiolo (2002) and Moss (1978). In a next step, development of taxon-specific indices from the knowledge gained in this analysis would be possible. Focusing only on variables that were significantly correlated with the species richness of individual TGs and applying individual weightings to variables, an improved taxon-specific assessment of habitat qualities could be conducted. For example, significantly correlated variables could be combined in additive models to predict the suspicious richness of certain taxonomic groups. In that case, an index describing the diversity of birds (BDI – Bird Diversity Index) could look like this (here without individual weightings of the variables used):

$$BDI = DBH + DBH\,sd + Height\,sd + Vol40 + DW\,d + DW\,s + N\,DC$$

Species richness in some TGs like hemipteran or formicidae was described by the FSI only in single regions or for certain types of forests. This might indicate that the habitat requirements of species within these TGs differ between forest types, or that there are regional differences in the pool of species within those TG, which can be analysed more specifically for individual

TGs in future studies. In addition, the species richness in these taxonomic groups may be driven by environmental or management influences that are not captured by forest structure. For example, Glaser (2006) and Wang *et al.* (2001) found that elevation and slope are important determinants for the diversity of formicidae, which were not considered in our study.

Species richness in other TGs such as orthopteran could not be described by structural variables used in the FSI. Possible explanations might be large home-ranges, the necessity of bordering open landscapes or structural attributes like access to food or further important elements that were not included in the analysis. It could also indicate (i) that they are not related to structure at all or (ii) that the developed forest structure index does not describe all aspects of stand structure. Marini *et al.* (2009), Littlewood (2008) and Schwab *et al.* (2002) showed the importance of agricultural management (amount of fertilizer, number of cuttings and nutrient input) for diversity of orthopteran on agricultural land bordering forest stands.

Therefore, we propose to use the data of the German Biodiversity Exploratories as a first guess for the intercept and suggest testing the FSI on further data to also better get a feeling whether absolute species numbers can be predicted.

3.6 Conclusion

Our analysis showed the possibility to use forest structural diversity, through FSI, to predict the changes in species richness of several taxonomic groups in three example regions of Germany or different types of forest stands and development phases. Thus, a tool is provided for the assessment of individual TGs in different types of forests in Germany. Other TGs could not be described by the FSI, indicating that further variables such as environmental factors (climate, topography, and soil types), management influences, and interaction with different land-use systems (e.g. agricultural land) may determine habitat quality of these groups.

In future, this information could be extrapolated to the whole of Germany, using the National Forest Inventory of Germany, or to other sites in central Europe to assess the potential habitat quality for individual species. Similarly, the forest structure index could be used to track changes in habitat diversity over inventory periods. This will allow getting a better understanding of how well FSI generalises and whether also the absolute level of species richness can be predicted in this system.

Using structural elements to predict or assess the habitat diversity for different TGs and by that the species richness would potentially support monitoring of different TGs through use of existing data.

Acknowledgements

This work was supported by a grant from the Ministry of Science, Research and the Arts of Baden-Württemberg (7533-10-5-78) to Jürgen Bauhus. Felix Storch received additional support through the BBW ForWerts Graduate Program. We like to thank all the experts of the German Biodiversity Exploratories for provision of their data-sets and their support in data management as well as the friendly team of the GBE, supporting this analysis.

We thank the managers of the three Exploratories, Katrin Hartwich, Sonja Gockel, Kerstin Wiesner and Martin Gorke for their work in maintaining the plot and project infrastructure, Christiane Fischer and Simone Pfeiffer for giving support through the central office, Britta König-Ries and Michael Owonibi for managing the central database, and Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Ingo Schöning and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories".

3.7 References

Abrahamsson M, Lindbladh M (2006) A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (Picea abies). In: Forest Ecology and Management 226 (1-3), S. 230–237. DOI: 10.1016/j.foreco.2006.01.046.

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. In: Forest Ecology and Management 258 (4), S. 525–537. DOI: 10.1016/j.foreco.2009.01.053.

Bazzaz FA (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology, 56(2), 485-488.

Bitterlich W (1948) Die Winkelzählprobe (The Angle-Count Sample Plot). Allgm. Forst-u. Holzwirtz. Ztg., 59: 4-5. In Forestry Abstracts (Vol. 10, p. 2314).

BMU (2011) Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit, Hrsg. 2011: Der Zustand der biologischen Vielfalt in Deutschland. Der Nationale Bericht zur FFH-Richtlinie. Silberdruck, Niestetal, 131 S.

Bütler R, Schlaepfer R (2004) Wie viel Totholz braucht der Wald?| Dead wood in managed forests: how much is enough?. Schweizerische Zeitschrift fur Forstwesen, 155(2), 31-37.

Davidowitz G, Rosenzweig ML (1998) The latitudinal gradient of species diversity among North American grasshoppers within a single habitat: a test of the spatial heterogeneity hypothesis. Journal of Biogeography, 25, 553–560.

Drapeau P, Nappi A, Imbeau L, Saint-Germain M (2009) Standing deadwood for keystone bird species in the eastern boreal forest: managing for snag dynamics. The Forestry Chronicle, 85(2), 227-234.

Fischer M, Bossdorf O, Gockel S, Hänsel F, Hemp A, Hessenmöller D (2010) Implementing large-scale and long-term functional biodiversity research: The biodiversity exploratories; Basic and Applied Ecology, 11 (2010), pp. 473-485

Gardner TA (2010) Monitoring Forest Biodiversity: Routledge.

Glaser F (2006) Biogeography, diversity, and vertical distribution of ants (Hymenoptera: Formicidae) in Vorarlberg, Austria. Myrmecologische Nachrichten, 8, 263-270.

Jung K, Kaiser S, Böhm S, Nieschulze J, Kalko EKV (2012) Moving in three dimensions. Effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. In: Journal of Applied Ecology 49 (2), S. 523–531. DOI: 10.1111/j.1365-2664.2012.02116.x.

Kahl T, Bauhus J (2014) An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nature Conservation, 7, 15.

Laiolo P (2002) Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. Folia Zoologica 51 (2), 121–128.

Lappi J, Bailey RL (1987) Estimation of the diameter increment function or other tree relations using angle-count samples.

Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, Krumm F, Vandekerkhove K (2018) Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, *84*, 194-207.

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity. A comprehensive multiscaled approach. Washington, DC: Island Press.

Lindenmayer DB, Margules CR, Botkin DB (2000) Indicators of Biodiversity for Ecologically Sustainable Forest Management. In: Conservation Biology 14 (4), S. 941–950. DOI: 10.1046/j.1523-1739.2000.98533.x.

Littlewood NA (2008) Grazing impacts on moth diversity and abundance on a Scottish upland estate. Insect Conservation and Diversity, 1, 142–150.

Lomolino MV (2000) Ecology's most general, yet protean pattern: the species–area relationship. Journal of Biogeography, 27, 17–26.

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology, 42, 594–598.

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton.

Mannan RW, Meslow EC (1984) Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. The Journal of wildlife management, 1219-1238.

Marini L, Fontana P, Battisti A, Gaston KJ (2009) Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland–forest mosaic: a multi-scale approach. Insect Conservation and Diversity, 2(3), 213-220.

McCoy ED, Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. Habitat structure: the physical arrangement of objects in space (ed. by Bell SS, McCoy ED and Mushinsky HR), pp. 3–27. Chapman & Hall, London

Mollet P, Zbinden N, Schmid H (2009) Steigende Bestandszahlen bei Spechten und anderen Vogelarten dank Zunahme von Totholz?| An increase in the population of woodpeckers and other bird species thanks to an increase in the quantities of deadwood?. Schweizerische Zeitschrift für Forstwesen, 160(11| 2009), 334-340.

Moning C, Müller J (2009) Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. Ecological indicators, 9(5), 922-932.

Moss D (1978) Diversity of woodland song bird populations. Journal of Animal Ecology 47, 521–527.

Müller J, Brandl R, Brändle M, Förster B, de Araujo BC, Gossner MM, Schmidt S (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. *Oikos*, *127*(6), 814-824.

Noss RF (1990) Indicators for Monitoring Biodiversity. A Hierarchical Approach. In: Conservation Biology 4 (4), S. 355–364. DOI: 10.1111/j.1523-1739.1990.tb00309.x.

Okland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation , 76, 297–310.

Pielou EC (1975) Ecological Diversity Wiley & Sons. New York.

Raison RJ, Flinn DW, Brown AG (2001) Application of criteria and indicators to support sustainable forest management: some key issues. CAB International, 2001. In: In Criteria and (2001).

Ralph CJ (1985) Habitat association patterns of forest and steppe birds of Northern Patagonia, Argentina. The Condor, 87, 471–483.

Ranius T, Ekvall H, Jonsson M, Bostedt G (2005) Cost-efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. In: Forest Ecology and Management 206 (1-3), S. 119–133. DOI: 10.1016/j.foreco.2004.10.061.

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Buscot F (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology.

Schoener TW (1976) The species-area relation within archipelagos: models and evidence from island land birds. In 16th international ornithological congress (pp. 629-642).

Schwab A, Dubois D, Fried PM, Edwards PJ (2002) Estimating the biodiversity of hay meadows in north-eastern Switzerland on the basis of vegetation structure. Agriculture, Ecosystems and Environment, 93, 197–209.

Simpson EH (1949) Measurement of diversity. Nature, 163, 688.

Sterba H (2008) Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. In: Forestry 81 (5), S. 587–597. DOI: 10.1093/forestry/cpn010.

Sullivan TP, Sullivan DS (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology, 38, 1234–1252.

Taboada Á, Tárrega R, Calvo L, Marcos E, Marcos JA, Salgado JM (2010) Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. In: Eur J Forest Res 129 (1), S. 31–45. DOI: 10.1007/s10342-008-0245-3.

Utschick H (1991) Beziehungen zwischen Totholzreichtum und Vogelwelt in Wirtschaftswäldern. Forstwissenschaftliches Centralblatt, 110(1), 135-148.

Wang C, Strazanac JS, Butler L (2001) Association between ants (Hymenoptera: Formicidae) and habitat characteristics in oak-dominated mixed forests. Environmental Entomology, 30(5), 842-848.

Zarnowitz JE, Manuwal DA (1985) The effects of forest management on cavity-nesting birds in northwestern Washington. The Journal of wildlife management, 255-263.

Chapter 4: Assessing the influence of harvesting intensities on structural diversity of forests in SW-Germany

Examples for timber harvesting:

a) cable-crane harvest (*), b) harvested timber (*), c) skidder (*), d) stand after single tree felling, regeneration of conifer-species settled (low HI) (*)

a)

b)

c)

d)

(*): pictures taken by Felix Storch

Assessing the influence of harvesting intensities on structural diversity of forests in SW-Germany

Felix Storch[1], Carsten F. Dormann[2], Gerald Kändler[3] and Jürgen Bauhus[1]

[1] Chair of Silviculture, University of Freiburg, D-79085 Freiburg, Germany

[2] Chair of Biometry, University of Freiburg, D-79085 Freiburg, Germany

[3] Department of Biometry, Forest Research Institute of Baden-Württemberg, D-79100 Freiburg, Germany

Author for correspondence

Felix Storch

Tel: +49-(0)761-203-8628

Fax: +49-(0)761-203-3781

Email: *felix.storch@waldbau.uni-freiburg.de*

Key words: *large-scale inventory, structural diversity index (FSI), harvesting intensity, changes in structural diversity*

Type of paper: research paper

4.1 Abstract

Structurally and compositionally diverse forests may be more robust than monocultures or one-layered stands in relation to biotic and abiotic stress and disturbances. There is further evidence that provision of a diversity of structural elements and many niches also leads to higher species diversity in forest ecosystems. These insights have led to the requirement to maintain or improve structural diversity to promote biodiversity in forests in many jurisdictions. At the same time, harvesting intensities may increase in coming decades to produce a significant part of woody biomass to support an increasing bioeconomy sector. Here, we address this issue and analyse to what extent harvesting intensity may influence forest structural diversity. For this purpose, a *Forest Structure Index* based on large-scale national forest inventory data of SW-Germany was previously developed. Based on these data, harvesting intensity was calculated for different types of forests (period 2002 – 2012) and its influences on structural diversity analysed. Our results show a relatively low impact of harvesting intensity on changes in structural diversity for most of the analysed types of forests. Only intense harvesting leads to a significant loss in structural diversity. For young stand development phases, a decrease in the developed index was found, indicating that harvesting intensities should not be intensified. Broadleaf-dominated stands show less potential to increase harvesting intensities than conifer-dominated stands before structural diversity is negatively impacted.

Our study shows that harvesting does not necessarily lead to a decrease in structural diversity and for some forest types harvesting intensity could be increased without a reduction in structural diversity. However, this increase relates to a theoretical potential that would have to be adjusted to meet the typical regulations and limitations that safeguard the sustainable management of forests.

4.2 Introduction

Structurally and compositionally diverse forests may be more robust than monocultures or one-layered stands in relation to biotic and abiotic stress and disturbances (Bauhus *et al.* 2017a, Thurm *et al.* 2016, Hooper *et al.* 2005). By providing many different niches and structural elements, a higher species richness is also assumed to be present, ('habitat heterogeneity hypothesis'; Jung *et al.* 2012, Tews *et al.* 2004, Simpson 1949). This can be achieved, for example, by implementing management strategies such as ‘retention forestry’, where the intentional protection and development of forest structural elements can support the maintenance of populations of different species (Gustafsson *et al.* 2012, Bauhus *et al.* 2009, Abrahamsson & Lindbladh 2006). At the same time, a growing bio-based economy strives to increase harvesting intensities in the future without compromising biodiversity (e.g. Bauhus *et al.* 2017b, BMBF 2014), which is required nowadays by many jurisdictions. This raises the question, how the intensity of harvesting can be safeguarded to avoid negative impacts on forest biodiversity, as it is not possible to monitor biodiversity in forests, directly. Presence or diversity of taxonomic groups can only be sampled in case studies for small areas, which leads to missing information across many sites. Therefore, the presence and the expression of structural elements are used as surrogates for information about the presence or the diversity of different taxonomic groups. By analysing changes in structural diversity of forests, possible changes in taxonomic diversity can be assessed, too.

So far, influences of harvesting activities on structural diversity of forests have not been analysed across many sites. However, these influences are the main reason for changes in forest structure which may in turn influence biodiversity (Kuuluvainen 2009, Raison *et al.* 2001, Lindenmayer *et al.* 2000). Impacts of harvesting intensities have been analysed for small areas (single forest stands), regarding changes in microhabitats (Michel & Winter 2009) or specific populations (Kern *et al.* 2006, Fredericksen *et al.* 1999). This lack of broad-scale assessments limits the generalization of these relationships for larger areas (Vandekerkhove *et al.* 2016, Gilliam 2002, Roberts *et al.* 2002). Further studies compared the level of structural diversity in managed forests with structural diversity in protected forest areas (Marchetti *et al.* 2017, Paillet *et al.* 2010, Okland *et al.* 2003). However, this approach has one important limitation. While the status of unharvested forest reserves can be reasonably well described and defined, these areas are compared with harvested forests that can cover a wide range of harvesting intensities ranging from clearfelling to single tree selections. Hence these simple comparisons provide no information on the influence of harvesting intensity on forest structure and biodiversity (Figure 4.1). Different harvesting intensities might have varying impacts on structural diversity of different types of forests. Therefore, NFI data of Baden-Württemberg was used in this study to include different types of forests and an inventory period of 10 years to analyse these impacts comprehensively across many sites.

Figure 4.1. Previous studies analysed differences in structural diversity between harvested and unharvested forests, excluding that harvesting intensities impact differently on structural diversity of forests

Earlier studies like Kahl & Bauhus (2014) or Schall & Ammer (2013) developed approaches to quantify forest management intensity to describe the level of human interference. To assess the intensity of forest management, an index on management intensity (ForMI) including the three criteria ‘proportion of dead wood showing signs of saw cuts’, ‘proportion of harvested tree volume’ and ‘proportion of tree species that are not part of the natural forest community’ (Kahl & Bauhus 2014) or changes of variables describing the level of naturalness (Winter *et al.* 2010) have been used. These approaches have been typically applied to small areas, where detailed information about the necessary variables was available. If the influence of harvesting intensity on forest biodiversity is to be assessed on a large scale, it may be determined more directly on the basis of inventory data.

Here, we used harvesting intensity calculated on the basis of national forest inventory (NFI) data as main variable to analyse changes in structural diversity of forests over large areas. Based on National Forest Inventory data of Germany for the state of Baden-Württemberg (SW-Germany, NFI_{2002} and NFI_{2012}), an index has been developed to assess the level of structural diversity of forests (chapter 2). To assess whether this index (*FSI* = *Forest Structure Index*) actually reflects measures of biodiversity, it was compared to diversities of different taxonomic groups, using data of the German Biodiversity Exploratories (Fischer *et al.* 2010). This data include information about presence / absence or the diversity of different taxonomic groups over three sample regions of Germany, including a management gradient (from intensively managed to unmanaged stands). Results showed the potential of the FSI to describe the presence / absence of different taxonomic groups in various types of forests (e.g. diversity of birds, bats, deadwood fungi, number of shrubs, ants or spiders, see chapter 3). We employed this index for our analysis because a) it describes structural- and species-diversity of forests b) it can be applied to large forest types / across many sites and c) calculations of harvesting intensities are performed on the same set of inventory data. By that, an assessment of the relationship between harvesting intensity and changes of structural diversity in different forest types for the period between the two national inventories (NFI_{2002} – NFI_{2012}) can be provided.

In this study, we used large-scale inventory data to assess the influence of different harvesting intensities on structural diversity in different types of forest ecosystems. The hypothesis was that increasing harvesting intensity would lead to a decrease in structural diversity of forests. However, no hypothesis was formulated on whether this decrease followed a linear or non-linear function. Based on these results, recommendations for future harvesting intensities in different forest types may be developed.

4.3 Material & Methods

4.3.1 Data basis

This study was based on 12.918 National Forest Inventory (NFI) plots in SW-Germany, covering approximately 1.371 million ha (hectares) of forest area and including a broad range of different types of forests, stand development phases and structural diversities. These plots were marked as 'forest' in NFI_{2002} and NFI_{2012} and were accessible at both inventories. An additional criterion was the presence of merchantable trees having DBH (diameter at breast height) larger than 7cm at NFI_{2002}. Plots were distributed over the whole state of Baden-Württemberg, Germany, representing 97.7% of all sampled plots in NFI_{2002} (chapter 2). Further information about the inventory (systematic grid, sampling design and background of this inventory) can be found at BMEL (2013) < https://www.bundeswaldinventur.de >.

4.3.2 Structural diversity index (FSI)

Based on data of NFI_{2002} and NFI_{2012} for the state of Baden-Württemberg, an index to assess the level of structural diversity of forests was established (chapter 2). Following the method described by McElhinny (2006), which was combined with the criterion 'aspects of structural diversity' (Sabatini *et al.* 2015), 11 variables representing 11 aspects of structural diversity were applied to calculate the FSI in a simple additive way, without weightings of individual variables (see supporting information I of chapter 4). This index was calculated at the plot-level and subsequently aggregated to forest types to obtain reliable estimates of structural diversity respectively the change in structural diversity. Index-values range between 0 and 1, where 0 implies 'lowest level of structural diversity' and 1 'highest level of structural diversity '. Distributions of FSI for the whole forest area of south-western Germany (NFI_{2002} and NFI_{2012}) are provided in the supporting information II of chapter 4. Further information about the development of this index can be found in chapter 2.

4.3.3 Calculation of harvesting intensities and relation to changes in structural diversity

Based on the same data-set (NFI_{2002} and NFI_{2012}), calculation of harvesting intensity (HI) was performed at the inventory plot-level. To analyse influences of harvesting intensities on changes in structural diversity of forests, different models were calculated and compared to each other. For statistical analysis, the statistic-software 'R' (Version 3.1.2) and package *mgcv* for *Generalized Additive Models* were used (Wood 2006), as these models can be used in a flexible way, including different numbers and functions for the applied predictor variables. A test for random effects caused by the sampling design of this inventory was included. Additionally, the packages *RODBC*, *ResourceSelection*, *randomForest* and *lmer* were used to calculate and compare different types of models to identify the model that describes best the relation between harvesting intensity and changes in structural diversity (see Table 4.1). Aggregation of plot data to harvesting classes (10%-intervals referred to standing timber volume of NFI_{2002}) was used to group various plots to increase the reliability of the analysis.

Table 4.1. Tested models to explain the relationship between harvesting intensity (HI) and changes in structural diversity (FSI-change)

Acronym	Model	Package	Explanation
loess	loess	RODBC	In addition to simply smoothing a curve, the R loess function can be used to impute missing data points
m	linear model	no package needed	lm is used to fit linear models
glm	generalized linear model	ResourceSelection	produces a generalized linear model for relationship HI - change of structural diversity (FSI)
gam	generalized additive model	mgcv	produces a generalized additive model for relationship HI - change of structural diversity (FSI)
RF	randomForest	randomForest	implements Breiman’s random forest algorithm for classification and regression (for harvesting classes)
HC	harvesting classes	No package needed	Harvesting classes for 10%-intervals, referred to the standing volume at NFI_{2002} to generate boxplots

We decided to represent HI as percentage of the standing timber volume (m^3 ha^{-1}) at NFI_{2002}. In this way, harvesting intensity is related to actual timber stocks and the actual intensity is described more accurately than by just volume per ha of harvested timber, which provides no information on harvesting intensity as a link to present timber stocks is missing. Harvesting intensity was calculated for the inventory period between NFI_{2002} and NFI_{2012}. For this period, a mean value of annual harvesting intensity (harvested timber volume divided by the duration of the inventory period for single plots) was determined because no information about actual dates of harvesting activities was available. These values were calculated on the basis of 12.918 forest plots, which were used to develop the FSI and its changes over a period of 10 years. This number of sampling plots is smaller than the total number that was used in the analyses of the NFI and hence the results may differ slightly from official NFI-analysis for the state of Baden-Württemberg. Changes in the structural diversity of forests (FSI-changes) are also expressed as percentage of NFI_{2002}-values to perform a link to the initial FSI-value at 2002.

4.4 Results

For the period 2002 – 2012, mean FSI-scores increased in all analysed types of forests, except for young stand development phases (Figure 4.2).

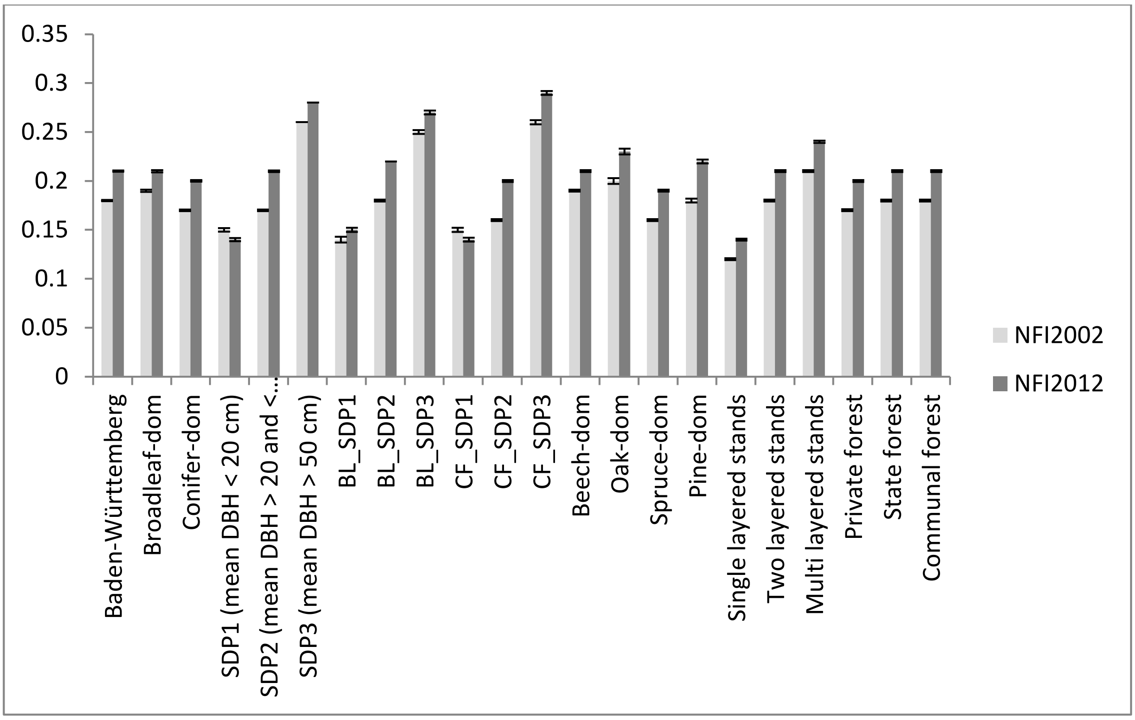


Figure 4.2. FSI-scores of NFI_{2002}, (light grey bars) and NFI_{2012}, (dark grey bars) for different forest types of SW-Germany; Error bars represent standard error of means. Differences between NFI_{2002} and NFI_{2012} are significant for an applied confidence level of 0.95 for all applied variables.

The calculation of FSI and HI at the plot-level includes a certain inaccuracy, caused by the sampling method for merchantable timber ('angle count method' - 'probability proportional to size'), (see also chapter 2, Sterba (2008), Lappi & Bailey (1987) and Bitterlich (1948)). This inaccuracy can be reduced by aggregation of single plots into harvesting classes, containing at least 15 sampling plots. Therefore, results on the interactions of harvesting intensity and changes in structural diversity (FSI) were expressed for classes of HI, using 10%-intervals and not for individual plots.

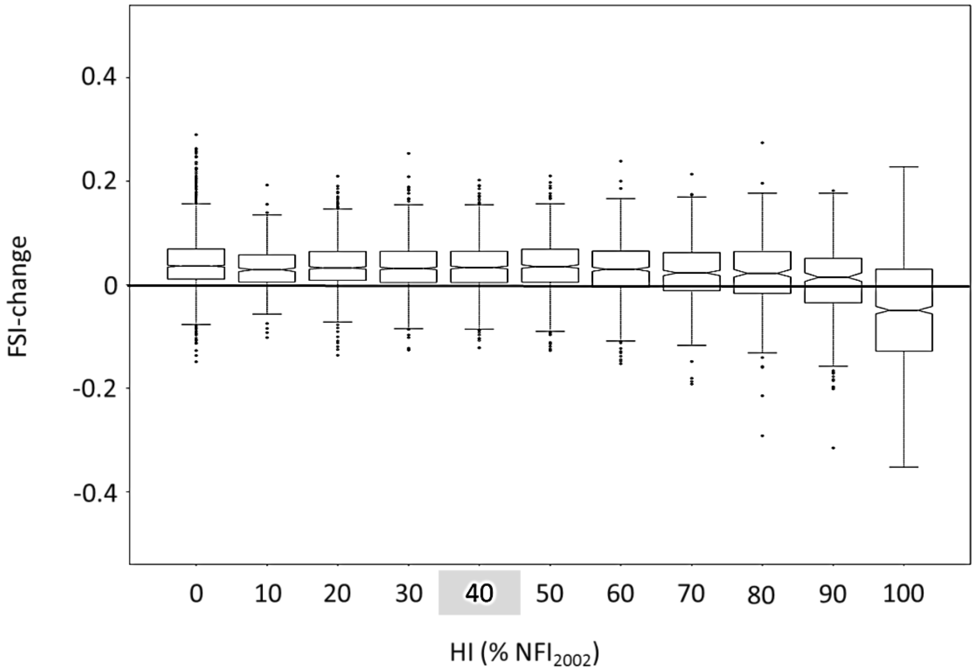


Figure 4.3. Boxplots for changes of the Forest Structure Index and harvesting intensity (in % of standing timber volume per ha of NFI_{2002}, depicted in 10%-intervals), based on inventory data for the entire forest area of Baden-Württemberg; The grey square on the x-axis indicates average harvesting intensity for the 10-year period between NFI_{2002} and NFI_{2012} (30.78%); black line indicates no change in the FSI.

Boxplots for all analysed types of forests are provided in the supporting information III of chapter 4. Surprisingly, a decrease in structural diversity was observed only for harvesting intensities greater than 90 % (Figure 4.3). Referred to the calculated HI of this inventory period, which was about 30 %, a large potential of additional woody biomass could be harvested without a reduction in structural diversity, theoretically. To understand the response of the FSI to harvesting intensity, the response of the individual variables contributing to the FSI were analysed and compared to each other across the gradient in harvesting intensity (Figure 4.4, Figure 4.5 and supporting information IV and V of chapter 4).

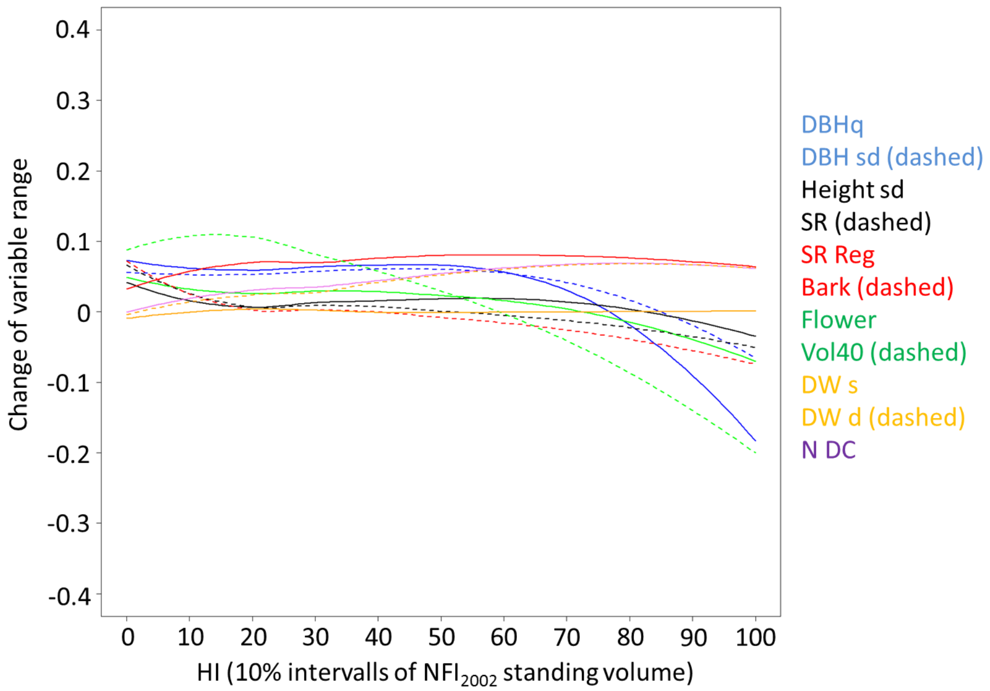


Figure 4.4. Changes in ranges of individual variables contributing to the FSI with harvesting intensity for national forest inventory plots from Baden-Württemberg; DBHq: quadratic mean diameter at breast height, DBH sd: standard deviation of diameter at breast height, Height sd: standard deviation of stand height, SR: species richness, SR Reg: species richness in regeneration layer, Bark: diversity of bark types, Flower: diversity of flowering trees, Vol40: occurrence of large living trees with a DBH ≥ 40 cm, DW s: mean DBH of standing deadwood, DW d: mean diameter of downed deadwood and N DC: number of decay classes.

Boxplots including more detailed information about changes of individual variables are provided in the supporting information IV of chapter 4. Changes in all individual variables used in the FSI for all analysed forest types can be found in supporting information V of chapter 4. As was the case for the full index, the influence of HI on most individual variables used in the FSI was quite small for the entire inventoried forest area of Baden-Württemberg, as well as for the different types of forests (Figure 4.4 and supporting information IV and V of chapter 4). A reduction of some structural variables like 'DBHq' or 'Vol40' was found only for harvesting intensities larger than 60 %. Hence, the small influence of HI on structural diversity can be attributed to small changes in the individual variables and not to contrasting responses of different variables that might counterbalance each other. For the sampling plots with no recorded harvest, changes in individual variables were quite heterogeneous over a period of 10 years. As shown in Figure 4.5, relatively small changes were found e.g. for the variables 'number of decay classes' and 'mean diameter of downed deadwood', which might be explained by the sampling design for deadwood variables (plot of 5 m radius). In addition, especially deadwood related variables might need longer time for changes, which is caused by natural processes (e.g. changes in decay classes need several years to decades to occur).

Expression of variables like 'species richness of the regeneration layer' or 'volume ha^{-1} of large living trees with a DHB ≥ 40 cm' showed relatively strong changes, indicating that these variables might change relatively fast or at least within a period of 10 years (e.g. after storm or drought).

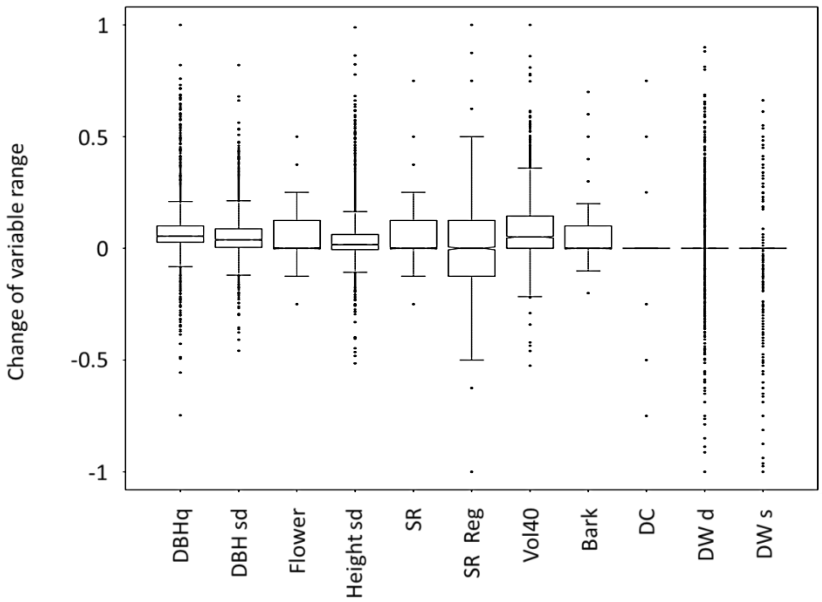


Figure 4.5. Relative changes in values for individual variable ranges of the structural diversity index for plots with no harvesting activity (HI = 0) in the most recent inventory period (recorded) for whole Baden-Württemberg; DBHq: quadratic mean diameter at breast height, DBH sd: standard deviation of diameter at breast height, Height sd: standard deviation of stand height, SR: species richness, SR Reg: species richness in regeneration layer, Bark: diversity of bark types, Flower: diversity of flowering trees, Vol40: occurrence of large living trees with a DBH ≥ 40 cm, DW s: mean DBH of standing deadwood, DW d: mean diameter of downed deadwood and N DC: number of decay classes

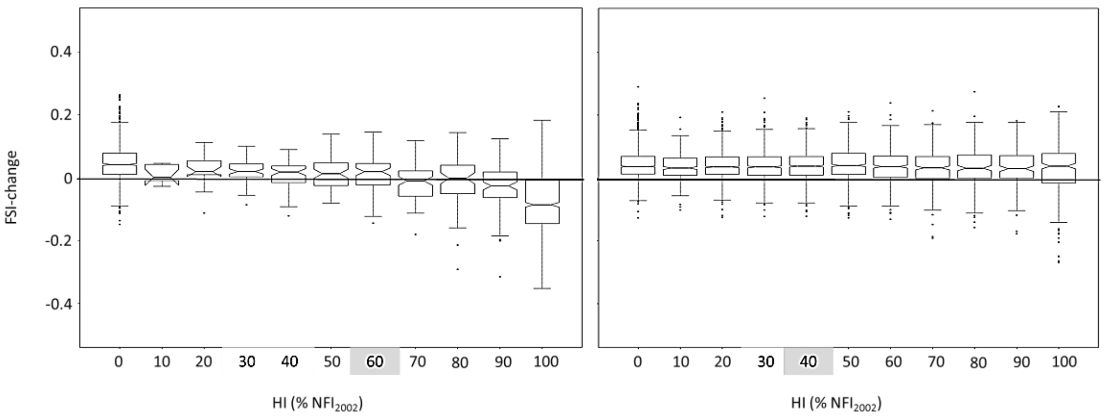


Figure 4.6. Boxplots for young (left, stand development phase 1 (mean DBH ≤ 20 cm)) and middle-aged stands (right, stand development phase 2 (mean DBH between 20 and 50 cm)); highlighted number (x-axis) indicates average harvesting intensity in the most recent inventory period (recorded) for whole Baden-Württemberg; black line indicates HI for FSI-Change = 0

Considering the two stand development phases (SDP1 and SDP2, Figure 4.6), as they represent the majority of inventory plots in Baden-Württemberg (about 84 % of all NFI plots), different influences of HI on structural diversity are obvious. A slight decrease in structural diversity is shown for young stands (SDP1 (mean DBH < 20 cm), left). Regarding middle-aged stands (SDP2 (mean DBH between 20 and 50 cm), right), HI seems to have less influence on the overall FSI-value.

Except for young stands (SDP1), HI could be theoretically increased without a loss in structural diversity. For these young stands, even low HIs lead to a decrease in structural diversity. A further result shows that conifer-dominated stands seem to be less influenced by HI than broadleaf-dominated forest stands. For coniferous stands (especially spruce in SDP2 (mean DBH between 20 and 50 cm)), HI may be increased before a loss in structural diversity occurs (supporting information III of chapter 4).

4.5 Discussion

4.5.1 Assessment of the NFI for questions on structural diversity and its development

Our results emphasise the potential of using large-scale inventory data such as the NFI of Germany to analyse the influence of harvesting intensity on structural diversity of different forest stands. Using the developed index for structural diversity (FSI), which is based on the same database, an assessment of the influence of previous harvesting intensities on the forest structural diversity can be performed. Following this approach, a theoretical potential amount of timber that can be harvested before a reduction in the overall structural diversity occurs, can be identified. This information should be understood as general trends for broad inventory strata such as forest types, or different types of ownership. Here, the highest amount of additionally harvestable timber, before a reduction of structural diversity sets in, was found in coniferous-dominated forests of Baden-Württemberg, mainly in middle-aged spruce stands (*Picea abies L.*). However, particular habitat attributes that are represented by individual variables of the forest structure index such as the 'quadratic mean diameter at breast height' or 'occurrence of trees with a DBH ≥ 40 cm' respond in a more sensitive way to harvesting intensity than e.g. 'standard deviation of stand height' or 'mean DBH of standing deadwood'. Therefore, limits to harvesting intensities may be set by changes in these more sensitive variables, if they present habitat for rare and endangered species like species depending on deadwood of large dimensions or large trees including habitat characteristics (Bußler *et al.* 2007, Bütler & Schlaepfer 2004).

One major outcome of our analysis is that harvesting does not always reduce the level of structural diversity. Especially harvesting intensities lower than 20 – 30 % of the standing volume in NFI_{2002} have led to a slight increase or maintenance of structural diversity in most types of forest ecosystems (supporting information III of chapter 4). This fact can be explained, for example, by a natural increase of tree species in the regeneration layer (often pioneer tree species) or an artificial increase in large dimensioned deadwood, which is supported by light to moderate harvesting intensities and modern management strategies such as 'retention forestry'. Another important result of our study is that some types of forests could be harvested more intensely than others before a loss in structural diversity sets in (e.g. older stands or stands with a higher structural complexity (double- or multi-layered) show a potential to increase HI whereas young stands seem to be affected more negatively). In unharvested forests, substantial changes in structural diversity are possible in particular following natural disturbances (e.g. Bauhus *et al.* 2017b, Thurm *et al.* 2016, Franklin *et al.* 2002). For example, through a windstorm deadwood is created, changes in light conditions occur that influence species richness in the regeneration layer and lead to establishment of pioneer tree species that increase tree species richness and the diversity of pollen and fruit production (Bauhus *et al.* 2017b, Hooper *et al.* 2005). More detailed information about the observed changes of individual variables applied in the FSI with increasing HI for all analysed forest types can be found in supporting information VI of chapter 4. In addition to the dynamics of structural elements caused by the above mentioned natural disturbances, the low impact of HI on FSI, as well as most of the applied individual variables within the FSI might be generally explained by the applied sampling method in the NFI (angle count sampling, chapter 2). This can be seen in the changes in forest structural diversity that were recorded in individual sampling plots, where actually no harvesting took place (Fig. 4.5). Here the changes in FSI at the plot level are more likely the result of the applied sampling method (angle count sampling); the mean FSI score for the class of unharvested plots however increased slightly (FSI-change of +0.04). For example, the highest increase in structural diversity for a single plot without recorded harvesting was 2186% (FSI_NFI_{2002}: 0.01, FSI_NFI_{2012}: 0.26), which was probably due to the sampling method and not by changes in natural conditions. This bias at the plot-level can be reduced by aggregation to forest types using mean values of the developed index and the included structural variables to assess the level of structural diversity and the changes over inventory periods. In addition, the calculated

HI can include biases that are caused by extrapolation volumes of sampled trees to hectare-values, which is necessary when using angle-count sampling and underlines the need for calculation of classes for harvesting intensities. As an extreme example on plot level, volume ha^{-1} at NFI_{2002}: 142 m³ ha^{-1}, harvested volume in this inventory period: 258 m³ ha^{-1}, leads to a harvesting intensity of 181 %, even the volume ha^{-1} at NFI_{2012} was 231 m³ ha^{-1}. Another reason for the low impacts of HI on structural diversity might be the relatively short period of ten years that was analysed in this study, combined with the lack of information about the date of harvesting activity. As a result, a certain inaccuracy is present for the calculation of HI (e.g. harvesting could have taken place directly before the inventory sampling of NFI_{2012}, as well as close to 10 years earlier, which will lead to different influences of harvesting on the dynamic development of structural variables and thus to differences in the calculated FSI for NFI_{2012}. Variables such as ‘quadratic mean diameter at breast height’ and ‘volume of trees with a diameter at breast height ≥ 40 cm’ could change immediately after harvesting, while variables such as the ‘number of decay classes’ and ‘mean diameter of downed deadwood’ might require years to decades to change in their expression. This uncertainty at the plot level can be compensated by aggregation to different types of forests, and thus increase the reliability of the results. However, influences of HI might affect structural diversity also over longer periods; therefore, this analysis should be continued for future NFIs to improve the quality of the FSI-statements by including ‘long-term changes’ of individual variables, too.

Although structural diversity is one important criterion when considering future harvesting-potential of forests, further limitations like forest reserves (protected areas without harvesting), levels of sustained yield or harvesting regulations (protection of soil or water, difficult terrain, ownerships) and the intention of forest owners, especially for privately owned forests, must be considered when calculating the 'actual' available above-ground biomass-potential of forests (Kilham *et al.* 2018, Kändler & Cullmann 2014, Mutz *et al.* 2002). For example, the highest amounts of standing timber volume are found in privately owned forests and are the result of extensive or no harvests over the last decades. This led to forest stands characterised by high amounts of deadwood or large living trees, as well as higher tree species richness in private compared to state-owned forests.

4.5.2 Assessment of harvesting intensities for period NFI_{2002} – NFI_{2012} in different types of forests

Our results show that HI can be increased without a loss in structural diversity for all analysed types of forests, except for young stands (SDP1). Additionally, harvesting intensity for most products was below the annual increment-level, as a result the aspect of sustainable timber yield will not be affected by an intensified harvesting activity (Kändler & Cullmann 2014, Eltrop *et al.* 2006). Some forest types can theoretically be harvested more intensely than others before a loss in structural diversity sets in. As shown in supporting information III of chapter 4, broadleaf-dominated forest stands have less potential than conifer-dominated stands to increase HI without a reduction in structural diversity. Beech- (*Fagus sylvatica* L.) and oak-dominated (*Quercus* spp.*)* stands seem to be more sensitive towards influences of HI on structural diversity than spruce- (*Picea abies* L.) or pine-dominated (*Pinus* spp.*)* stands. These differences are possibly caused by different stand characteristics and therefore by changes in individual variables such as 'species richness in the regeneration layer' (caused by a higher species richness of the regeneration layer in broadleaf-dominated stands), 'diameter at breast height of standing deadwood', 'standard deviation of stand height' (caused by the fact that broadleaf-dominated stands are more often multi-layered stands and therefore show a higher expression of this variable as conifer-dominated stands, which are often one-layered stands) and 'diversity of bark types'. All other structural variables had more positive changes with increasing HI in broadleaf-dominated stands than in coniferous-dominated stands (supporting information VI of chapter 4). Some individual structural variables seem not to be affected by harvesting (e.g. standing deadwood or flower diversity). One could argue that these variables should therefore be dropped from the index. Keeping insensitive variables in the index could blur the impact of harvesting on the FSI. That would be true for percent changes but not for absolute changes. However, a reduction of variables to the ones being sensitive to HI was not performed, because all included variables cover an important aspect of structural and taxonomic diversity and should be included in a comprehensive assessment of diversity, even if at this stage, no change was recorded over one period.

4.5.3 Recommendations for future harvesting intensities in different forest types

The results of our analysis suggest that most forest types, especially conifer-dominated stands, could be harvested more intensely in future without a loss in structural diversity. For example, an increase of HI in spruce-dominated stands during the stand developmental phase 2 (diameter at breast height between 20 and 50 cm), appears to be possible. Considering that many of these forests have been targeted for ecological restoration and adaptation to climate change but also that many are already being impacted by insects such as bark beetles and or fungi such as *Fomes annosus* on *Picea abies* L., the approach of harvesting more spruce timber biomass than the sustainable yield could be sensible in an ecological and economic way (Teuffel *et al.* 2005). This potential might be available only for a few decades before changes in age-classes lead to a decrease of available spruce-timber of stand development phase 2 (middle-aged spruce-dominated stands). The small proportion of spruce in regeneration, as well as in young age-classes intensifies further this problem (Polley & Kroiher 2017).

Additionally, young stands (stand development phase 1) seem to be harvested quite intensely already and HI should not be increased to maintain the level of structural diversity (supporting information III of chapter 4).

Impacts of harvests on individual variables included in the Forest Structure Index are quite heterogeneous and should be assessed separately. For example, the amount of downed deadwood might increase after harvests, which favours the deadwood depending flora and fauna. As timber harvests produce mainly small-dimensioned deadwood, especially taxonomic groups depending on these small diameters and early decay classes of deadwood are supported. Other variables like the occurrence of large trees with a diameter at breast height ≥ 40 cm might be reduced by harvests, so populations of species depending on these habitats might also be reduced. Therefore, influences of harvests or harvesting intensity can have totally different impacts on single taxonomic groups or individual species within taxonomic groups.

A further aspect that has to be considered is the ecological sustainability of harvesting activities, which is recommended by forest experts and is binding by policy guidelines for modern harvesting strategies but not taken into account in this analysis (Loiskekoski 1993). Focusing on this criterion, most types of forests are used below the level of increment, allowing a theoretical increase of HI. Given that most forests in Baden-Württemberg are relatively young, current increment growth rates are high. However, growth rates will decline in the coming decades, as increment-values in later stand development phases or age-classes are lower (Polley & Kroiher 2017).

Regarding the beta- and gamma-diversity of taxonomic groups in forests, a mixture of high and low FSI-values at landscape-level would be recommended, as underlined by the analysis on data of the German Biodiversity Exploratories (chapter 3, Schall *et al.* 2018, Simpson 1949). Some taxonomic groups like arachnidae, bats or hymenoptera seem to prefer structurally poor stands (low FSI-scores), whereas taxonomic groups like birds or deadwood fungi prefer structurally rich ecosystems (high FSI-scores). Even within a taxonomic group, habitat demands of single species might differ drastically, which therefore need to be analysed separately. For example, the group of coleoptera can be separated into different sub-groups like saproxylic beetles, ground beetles or burying beetles. Leston *et al.* (2018) showed that long-term changes after different harvesting scenarios can provide habitats for different bird species and thus increase the overall species richness when compared to unharvested stands. Therefore, to keep species diversity at the highest possible level, a broad spectrum in the expression of structural elements and by that structural diversity should be present at the landscape-level (Schall *et al.* 2018, Sullivan & Sullivan 2001, Okland 1996).

The main focus of this study was on the influence of harvesting intensity on forest structural diversity, whereas harvesting methods were not considered because there is no relevant information available in the NFI-data of Germany. Different harvesting methods such as selection cutting (e.g. single tree felling or group-wise felling) or clear cuts lead to differences in structural diversity of forests too (Kuuluvainen 2009, Rosenvald & Lohmus 2008, Siira-Pietikäinen *et al.* 2001). Retention forestry can support structural diversity by maintaining certain structural elements or creating them artificially (e.g. standing dead trees or high stumps; Gustafsson *et al.* 2012, Bauhus *et al.* 2009, Abrahamsson & Lindbladh 2006). It would be very valuable, if inventories provided information about the influences of different harvesting and regeneration methods on forest structural diversity since this information could be used to evaluate these management systems on a large scale.

4.6 Conclusion

Our results show the general possibility to use large-scale inventory data like the NFI of Germany to analyse the influence of harvesting intensity on structural diversity of different forest stands. Using the developed FSI to assess the level of structural diversity, which is based on the same data basis, an assessment of previous harvesting intensities on structural diversity can be carried out. The relatively low impacts of HI on the FSI, as well as the included variables over a period of 10 years were surprising. The analysis of the influence of HI on structural diversity should be continued considering the medium-to long-term influence, which may be different from the short-term responses.

The low impact of HI on structural diversity shown in this analysis might be different when applying forest inventories, using fixed radius plots, which are not available on large-scale for Baden-Württemberg or Germany. Therefore, to produce a more robust statement of this analysis, application of the FSI and its changes with increasing HI should be analysed on enterprise inventory data, as well as for upcoming NFIs to extend the assessment period and by that, the quality of the statement.

To conclude, this index can be used to assess the level of structural diversity over different types of forests, as well as its changes over periods of 10 years caused by harvesting activities and thereby support forest monitoring and also political decisions on forest management intensities across many sites. Although a certain inaccuracy is included at a small spatial scale and through the quantification of harvesting activities (caused by the sampling design of the NFI and the inaccuracy of harvesting dates), this analysis can be used to assess changes in forest structural diversity across many sites.

Acknowledgements

This work was supported by a grant from the Ministry of Science, Research and the Arts of Baden-Württemberg (7533-10-5-78) to Jürgen Bauhus. Felix Storch received additional support through the BBW ForWerts Graduate Program.

4.7 References

Abrahamsson M, Lindbladh M (2006) A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (Picea abies). In: Forest Ecology and Management 226 (1-3), S. 230–237. DOI: 10.1016/j.foreco.2006.01.046.

Bauhus J, Kouki J, Paillet Y, Asbeck T, Marchetti M (2017a) How does the forest-based bioeconomy impact forest biodiversity? In: Winkel G (ed.) Towards a sustainable European forest-based bioeconomy – assessment and the way forward. What Science Can Tell Us 8, European Forest Institute, pp. 67-76. ISBN 978-952-5980-41-7

Bauhus J, Forrester DI, Gardiner B, Jactel H, Vallejo R, Pretzsch H (2017b) Ecological Stability of Mixed-Species Forests. In Mixed-Species Forests (pp. 337-382). Springer Berlin Heidelberg.

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. In: Forest Ecology and Management 258 (4), S. 525–537. DOI: 10.1016/j.foreco.2009.01.053.

Bitterlich W (1948) Die Winkelzählprobe (The Angle-Count Sample Plot). Allgm. Forst-u. Holzwirtz. Ztg., 59: 4-5. In Forestry Abstracts (Vol. 10, p. 2314).

BMEL (2013): The National Forest Inventory, < https://www.bundeswaldinventur.de > (10.07.2018)

Bußler H, Blaschke M, Dorka V, Loy H, Strätz C (2007) Auswirkungen des Rothenbucher Totholz- und Biotopbaumkonzepts auf die Struktur-und Artenvielfalt in Rot-Buchenwäldern.

Bütler R, Schlaepfer R (2004) Wie viel Totholz braucht der Wald?| Dead wood in managed forests: how much is enough? Schweizerische Zeitschrift fur Forstwesen, 155(2), 31-37.

Eltrop L, Moerschner J, Härdtlein M, König A (2006) Bilanz und Perspektiven der Holzenergienutzung in Baden-Württemberg.

Fischer M, Bossdorf O, Gockel S, Hänsel F, Hemp A, Hessenmöller D (2010) Implementing large-scale and long-term functional biodiversity research: The biodiversity exploratories; Basic and Applied Ecology, 11 (2010), pp. 473-485

Fredericksen TS, Ross BD, Hoffman W, Morrison ML, Beyea J, Bradley NJ, Lester MB, Ross E (1999) Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. In: Forest Ecology and Management 116 (1-3), S. 129–139. DOI: 10.1016/S0378-1127(98)00452-6.

Gilliam FS (2002) Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. In: Forest Ecology and Management 155 (1-3), S. 33–43. DOI: 10.1016/S0378-1127(01)00545-X.

Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, Neyland M (2012) Retention forestry to maintain multifunctional forests: a world perspective. BioScience, 62(7), 633-645.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning. A consensus of current knowledge. In: Ecological Monographs 75 (1), S. 3–35. DOI: 10.1890/04-0922.

Jung K, Kaiser S, Böhm S, Nieschulze J, Kalko EKV (2012) Moving in three dimensions. Effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. In: Journal of Applied Ecology 49 (2), S. 523–531. DOI: 10.1111/j.1365-2664.2012.02116.x.

Kahl T, Bauhus J (2014) An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nature Conservation, 7, 15.

Kändler G, Cullmann D (2014) Der Wald in Baden-Württemberg. Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Forstliche Versuchs-und Forschungsanstalt Baden-Württemberg, Freiburg.

Kern CC, Palik BJ, Strong TF (2006) Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. In: Forest Ecology and Management 230 (1-3), S. 162–170. DOI: 10.1016/j.foreco.2006.03.034.

Kilham P, Kändler G, Hartebrodt C, Stelzer AS, Schraml U (2018) Designing Wood Supply Scenarios from Forest Inventories with Stratified Predictions. *Forests*, *9*(2), 77.

Kuuluvainen T (2009) Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe. The Complexity Challenge. In: AMBIO: A Journal of the Human Environment 38 (6), S. 309–315. DOI: 10.1579/08-A-490.1.

Lappi J, Bailey RL (1987) Estimation of the diameter increment function or other tree relations using angle-count samples.

Leston L, Bayne E, Schmiegelow F (2018) Long-term changes in boreal forest occupancy within regenerating harvest units. In: Forest Ecology and Management. DOI: 10.1016/j.foreco.2018.02.029.

Lindenmayer DB, Margules CR, Botkin DB (2000) Indicators of Biodiversity for Ecologically Sustainable Forest Management. In: Conservation Biology 14 (4), S. 941–950. DOI: 10.1046/j.1523-1739.2000.98533.x.

Loiskekoski M (1993) Ministerial Conference on the Protection of Forests in Europe, 16-17 June 1993 in Helsinki. In Ministerial Conference on the Protection of Forests in Europe 1993: Helsinki, Finland). Ministry of Agriculture and Forestry, Ministerial Conference on the Protection of Forests in Europe, Liaison Unit in Helsinki.

Marchetti M, Bastrup-Birk A, Parviainen J, Santopuoli G, Vizzarri M, Jump A, Sotirov M (2017) The state of biodiversity in Europe's forest systems.

McElhinny C, Gibbons P, Brack C (2006) An objective and quantitative methodology for constructing an index of stand structural complexity. In: Forest Ecology and Management 235 (1-3), S. 54–71. DOI: 10.1016/j.foreco.2006.07.024.

Michel AK, Winter S (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. In: Forest Ecology and Management 257 (6), S. 1453–1464. DOI: 10.1016/j.foreco.2008.11.027.

Mutz R, Borchers J, Becker G (2002) Forstliches Engagement und forstliches Engagementpotenzial von Privatwaldbesitzern in Nordrhein-Westfalen - Analyse auf der Basis des Mixed-Rasch-Modells. Analysis of current and potential commitment of private forest owners in North Rhine-Westphalia based on the mixed Rasch model. In: Forstwissen Centr 121 (1), S. 35–48. DOI: 10.1046/j.1439-0337.2002.01039.x.

Okland TK, Rydgren RH, Økland K, Storaunet O, Rolstad J (2003) Variation in environmental conditions, understorey species number, abundance and composition among natural and managed Picea-abies forest stands. Forest Ecology and Management 177: 17–37

Okland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation, 76, 297–310.

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Kanka R (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation biology, 24(1), 101-112.

Polley H, Kroiher F (2017) Nadelwälder in Deutschland. In Pro Wald, March 2017, S. 4-7.

Raison RJ, Flinn DW, Brown AG (2001) Application of criteria and indicators to support sustainable forest management: some key issues. CAB International, 2001. In: In Criteria and (2001).

Roberts MR, Zhu L (2002) Early response of the herbaceous layer to harvesting in a mixed coniferous–deciduous forest in New Brunswick, Canada. In: Forest Ecology and Management 155 (1-3), S. 17–31. DOI: 10.1016/S0378-1127(01)00544-8.

Rosenvald R, Lohmus A (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management, 255(1), 1-15.

Sabatini FM, Burrascano S, Lombardi F, Chirici G, Blasi C (2015) An index of structural complexity for Apennine beech forests. In: iForest 8 (3), S. 314–323. DOI: 10.3832/ifor1160-008.

Schall P, Ammer C (2013) How to quantify forest management intensity in Central European forests. European Journal of Forest Research, 132(2), 379-396.

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Buscot F (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology.

Siira-Pietikäinen A, Pietikäinen J, Fritze H, Haimi J (2001) Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. Canadian Journal of Forest Research, 31(1), 88-99.

Simpson EH (1949) Measurement of diversity. Nature, 163, 688.

Sterba H (2008) Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. In: Forestry 81 (5), S. 587–597. DOI: 10.1093/forestry/cpn010.

Sullivan TP, Sullivan DS (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology, 38, 1234–1252.

Teuffel K, Baumgarten M, Hanewinkel M, Konold W, Sauter UH, Spiecker H, Wilpert K (Eds.). (2005) Waldumbau: für eine zukunftsorientierte Waldwirtschaft. Springer-Verlag.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity. The importance of keystone structures. In: Journal of Biogeography 31 (1), S. 79–92. DOI: 10.1046/j.0305-0270.2003.00994.x.

Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. In: Forest Ecology and Management 376, S. 205–220. DOI: 10.1016/j.foreco.2016.06.020.

Vandekerkhove K, Thomaes A, Crèvecoeur L, Keersmaeker L de, Leyman A, Köhler F (2016) Saproxylic beetles in non-intervention and coppice-with-standards restoration management in Meerdaal forest (Belgium). An exploratory analysis. In: iForest 9 (4), S. 536–545. DOI: 10.3832/ifor1841-009.

Winter S, Fischer HS, Fischer A (2010) Relative quantitative reference approach for naturalness assessments of forests. Forest ecology and management, 259(8), 1624-1632.

Wood SN (2006) Generalized additive models. An introduction with R. Boca Raton: Chapman & Hall/CRC (Texts in Statistical Science).

5. Synthesis

The results of this study show that the structural diversity index, originally developed for large-scale forest inventory data of Baden-Württemberg, can be utilised to successfully assess structural diversity. Changes over 10-year periods can be analysed and recommendations for suitable harvesting intensities taking into account tolerable changes in forest structure at the level of forest types can be developed. Our results show the possibility of using structural variables of forests, derived from large-scale inventory data of Germany, to describe species diversity of tested taxonomic groups such as birds or deadwood fungi.

A tool for assessing the level of structural diversity across many sites has been missing for interpreting biodiversity-relevant aspects of national forest inventories. The developed FSI can be used to support decision-making processes or societal debates on the use of forests. In general, harvesting activities do not necessarily influence the level of structural diversity negatively. In some of the forest types analysed, low harvesting intensities could even have slightly positive effects on structural diversity and thereby on species diversity. These results indicate that an increase of harvesting intensity in some types of forests is possible and that this additional amount of harvested woody biomass from forests could be used to support the growing bioeconomy sector in Baden-Württemberg.

5.1 Assessment of the NFI for questions on structural diversity

Most of the relevant aspects of structural diversity that are considered important for a comprehensive assessment of structural elements in forests by several studies (e.g. Köhl 1996, Tomppo 1996), have been sampled since 2002 within the NFI of Germany. Only a few aspects that are relevant for structural diversity have not been included, such as information on the litter layer (for example litter composition or litter thickness) or microhabitats. Some microhabitats were assessed in the NFI_{2012} but could not be included in this analysis, because of missing data for (or: because they did not exist in) NFI_{2002}. In some cases, surrogates are used to assess missing information. For instance, large trees (DBH $\geq$ 40 cm) are used as the surrogate for habitat tree characteristics such as hollows, cracks, single dead branches or crown deadwood. This can be justified by the distribution of trees showing habitat characteristics within NFI_{2012} (see also chapter 2, supporting information VIII and relevant studies e.g. by Paillet *et al.* 2017, Regnery *et al.* 2013, Vuidot *et al.* 2011). It is also important to mention that the German NFI was initially not developed to support biodiversity monitoring. The main reason for the implementation of the NFI was to assess the standing tree volume in different types of forests, its changes over periods of ten years, changes in tree species and to provide information about the stocks and harvesting potential of different timber products (Polley & Kroiher 2017, Kändler & Cullmann 2014, Polley 2005). In the last two NFIs of Germany (2002 and 2012), variables describing structural diversity have been included, which were used for example, to assess the level of naturalness of forest stands. This indicates the importance of this growing field, which will hopefully be further continued in upcoming NFIs (Polley 2010, Rondeux 1999, Tomppo 1996). This provides the basis for the calculation of measures of structural diversity, which can be produced instantly and attached to the NFI-database (website), as well as analyses of the development over 10-year periods for the whole forest area of Germany or federal states. The long-term changes in structural diversity might be of particular interest, but have not been analysed in previous studies, possibly owing to financial limitation, unavailability of broad data sets or the duration of projects. However, information on changes in structural diversity is particularly important to guide forest management and to report about its effects in an objective and comprehensive way. This information can be provided instantly by the NFI of Germany, which underlines the importance of national inventories and tools such as the developed FSI for upcoming questions on diversity in forests.

5.1.1 Inventory design

One strength of the German NFI as a basis to develop an index on structural diversity is the variety and range of sampled structural elements, which is needed to assess structural diversity comprehensively (Rondeux 1999, Tomppo 1996). The sampling is repeated in 10-year periods across many sites, so changes of structural diversity can be analysed for different types of forest stands. These changes can be tracked, because sampling plots and trees are re-sampled. In addition, sampling plots are marked invisibly to exclude a biased treatment of the area, which is needed to capture the real conditions of forest stands. These inventory-related aspects show the suitability of the NFI to develop a structural diversity index.

An important limitation of the German NFI results from the sampling design for trees with a diameter at breast height (DBH) larger than 7 cm at the plot-level. It is based on angle count sampling with a basal area factor of 4, where selection of an individual tree depends on its DBH and its distance to the centre of the sampling plot. This leads to a loss of information at the plot-level, but the large number of sampling plots within a given type of forest (forest stand) leads to accurate values at the stratum level consisting of a sufficiently large number of plots, e.g. the forest-type (chapter 3, Sterba 2008, Lappi & Bailey 1987, Bitterlich 1948). To analyse the structural diversity of forests at the level of (small) individual stands or at the plot-level, a different sampling method, such as sampling with fixed radius circles or complete inventories, is necessary but not available across many sites of Baden-Württemberg. These inventory methods use larger sampling plots and thereby include a higher number of trees, which leads to more accurate results at the plot-level or for small forest stands. This limits the transferability of knowledge about habitat demands for different taxonomic groups gained from the German Biodiversity Exploratories to NFI data, because information from the exploratories is provided at the plot-level (1 ha) but has to be transferred to stand-level of the NFI including a larger number of sampling plots to produce more reliable results on structural elements and thereby on habitat quality for different taxonomic groups (Figure 5.1). Also the level of correlation between taxonomic groups and FSI will not be as high if sampled by the angle count method of the NFI instead of a 1 ha inventory. This discrepancy might lead to difficulties when transferring information about TGs (taxonomic groups) to NFI-data and therefore also across many sites, as NFI-plots only cover a small area which might not be representative for the surrounding forest stand.

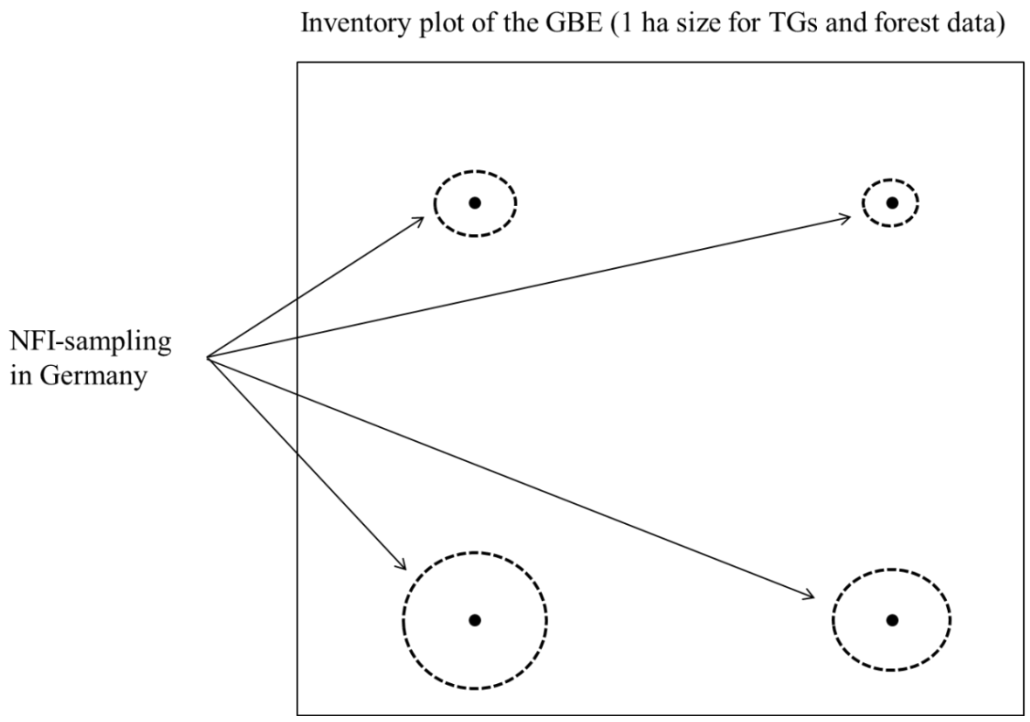


Figure 5.1. Sampling design of the GBE (inventory plot of 1 ha size) and angle-count samplings of the German NFI (variable in size)

Therefore, statements about habitat quality of individual taxonomic groups can only be given on stand-level and not on plot-level. Further research is required on this topic, underlining the importance to assess habitat qualities for different taxonomic groups on a large scale and its changes over periods of 10 years.

Sampling of rare elements such as deadwood within a single plot of 5 m radius is also problematic, because deadwood is not evenly distributed in forest stands but is often spatially clumped (Meyer 1999). Plots of small size may not capture the 'real' situation or the right amount of deadwood (Rondeux & Sanchez 2010). Extrapolation from sample plot areas to hectare values (multiplied by a factor of 127) may thus easily lead to an over- or underestimation while the handling of these extreme values is quite challenging in subsequent analyses. Therefore, mean diameter was chosen in the presented analysis for standing and downed deadwood, which does not have to be extrapolated to hectare values but still provides enough information on the variable / aspect. The correlation between mean diameter of downed deadwood and volume ha^{-1} of downed deadwood was high (R^2 = 0.97) as shown in the supporting information IV of chapter 2. Furthermore, the range of mean diameter was between 0 and 96 cm and the range of calculated volume ha^{-1} between 0 and 1714 m^3 ha^{-1}. The idea to increase the radius of deadwood plots to improve the accuracy of sampling is unlikely to be practical due to financial limitations. Therefore, a different sampling method has been recommended - e.g. 'Line Intersect Sampling' to improve data-quality, even if comparability to previous NFIs is lacking (Ritter & Saborowski 2012, Jordan *et al.* 2004, Buckland *et al.* 2001).

To exclude outliers (extreme values caused by the sampling design), threshold-values based on the NFI-dataset and literature were applied. These values can also be used for other inventory designs such as complete inventories or inventories using fixed radius circles; if necessary, an adaption of new threshold-values for the considered ecosystems is easily possible (e.g. if structural variables show significantly higher or lower values than in the presented study for Baden-Württemberg or Germany).

5.1.2 Harvesting intensity and limitations of the NFI and alternative data sets

Analysis of the influence of harvesting intensity on changes of the structural diversity index is challenging, because of the angle count sampling method and the small sampling plots for deadwood. This bias at the plot-level can be reduced by aggregation of harvesting intensity and FSI data at the level of larger strata, such as forest types, so that changes in structural diversity can be related to mean harvesting intensities. These changes in the FSI should be analysed for more than one period to include long-term changes in structural elements that might affect changes in structural diversity of forests. Considering the mean period for harvesting leads to an inaccuracy, because the actual harvesting could have taken place up to 5 years earlier or later, which might lead to differences in the dynamic of structural elements. For example, impacts of harvests on variables such as species richness in the regeneration layer are considered long-term changes, because it might take several months to years for new species to establish in the harvested area. Impacts on variables such as the occurrence of large trees are considered as short-term changes, because harvests affect the structural elements of forests immediately. This fact - combined with the sampling method of angle count sampling - also leads to inaccuracies in the calculated harvesting intensity (HI), assuming a growth of harvested trees until the middle of the period, which leads in some cases to HIs > 100% of standing volume at NFI_{2002}, even if in reality no clear-cut of the forest took place at the plot. To analyse the influence of harvesting intensities on structural diversity of forests, statistical models such as linear and generalized additive models were used. To increase the reliability of the results, harvesting classes of 10% (referring to the standing volume of NFI_{2002}) were analysed for changes in the structural diversity index. Both methods showed a relatively low impact on the structural diversity of forests. Therefore, 10% classes were used to analyse the influence of harvests on structural diversity.

Results represented in chapter 4 show a certain potential to increase harvesting intensities without a reduction in structural diversity for all analysed forests types (except for young conifer-dominated stands). However, this potential is only theoretical and therefore should be regarded with caution. Further restrictions, including the protection status of areas, limitations of harvesting activities or different ownership were not taken into account. In addition, habitat quality as expressed by structural elements in the FSI is referred to all tested taxonomic groups including rare, endangered and common species to assess the overall diversity of taxonomic groups in forest ecosystems. Especially the rare and endangered species might only require some structural elements (such as large amounts of deadwood or the occurrence of large living trees), which are only one aspect of the overall FSI-score. The actual harvesting intensity might therefore be adjusted to the habitat needs of particular species or groups of species, as for example shown for wood grouse (*Tetrao urogallus*) in the work by Braunisch & Suchant (2013). Therefore, the actual potential may not be as high as the calculated theoretical potential in this study. For a comprehensive assessment of the influence of harvesting intensity on the structural diversity of forests, a second inventory-period of 10 years should be included in the analysis to capture long-term changes.

The idea to use forest enterprise / management district inventory data, which contain more precise information on harvesting activities and are based on forest sampling in fixed radius plots, was rejected because a) databases do not include precise information on harvesting intensities for individual stands (caused by the raster of the sampling design), b) they are limited by small spatial coverage (enterprises level) and are only available for state-owned forests (permanent inventories) and parts of the community-owned forests (temporary inventories) (about 62% of the forest area in Baden-Württemberg).

Calculation of FSI-changes for forest reserves showed comparable results to changes within the NFI, indicating that the sampling method (angle count sampling) is also suitable to analyse changes in structural diversity (see also results and discussion in chapter 4).

In general, the FSI in broadleaf-dominated stands (Figure 5.2, left) seems to be slightly more negatively affected by increasing harvesting intensity than in conifer-dominated stands (Figure 5.2, right).

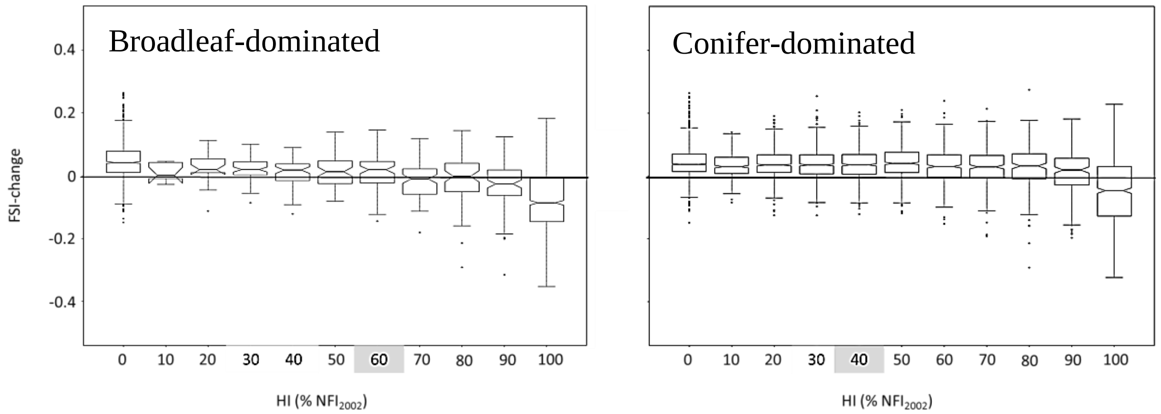


Figure 5.2. Boxplots for changes of the FSI; highlighted number (x-axis) indicates average harvesting intensity for the period NFI_{2002} – NFI_{2012}; black line indicates HI for FSI-Change = 0

Analysing changes in individual variables with increasing harvesting intensity for these two types of forest ecosystems (supporting information V, chapter 4) showed that most of the variables included in the FSI were affected slightly more negatively by increasing harvesting intensities in broadleaf-dominated stands than in conifer-dominated stands. These stands also include significantly higher numbers of trees with habitat structures (about 9 trees ha^{-1})[2], compared to conifer-dominated stands (about 3 trees ha^{-1})[2], which corresponds with the results and recommendations for harvesting intensities of our study to maintain or increase the

[2] Number of habitat trees calculated using data of NFI_{2012} for the state of Baden-Württemberg by Storch 2018

level of diversity. Young and old stands are affected more negatively by increasing harvesting intensities than middle-aged stands, especially spruce-dominated stands, which provide the highest potential to increase harvesting intensity without a loss in structural diversity. This might be explained by different stand characteristics such as the number of stand layers, species richness of regeneration or the amount of standing and downed deadwood. These differences might also explain the differences between broadleaf- and conifer-dominated stands. A separation into ownerships showed no differences for private, state, and municipal / communal forests regarding harvesting-related changes of the FSI.

5.2 Assessment and application of the FSI

To develop an index for a comprehensive assessment of structural diversity, a set of data including many different aspects of diversity is required (e.g. Sabatini *et al.* 2015, McElhinny *et al.* 2006). Data of the National Forest Inventories of Germany include most of the relevant information required to analyse structural diversity comprehensively and were therefore used in this analysis (Rondeux 1999, Tomppo 1996). To improve the developed diversity index, previously missing aspects can easily be adapted to the FSI when the relevant data become available. In addition, a reduced version of the FSI can also be easily applied to assess the level of structural diversity, if variables are missing (e.g. in other European NFIs). Further details about the potential to modify the FSI are provided in chapter 2. Therefore it is important to compare only FSI-scores that are calculated on the same structural variables. An adjustment of the FSI to other forest ecosystems that are characterised by a different expression of stand attributes (e.g. larger dimensions of trees, higher amount of standing or downed deadwood, etc. – as can be found in primeval beech forests or forest reserves, see for example Tabaku (2000)) is also easily possible by adaption of threshold-values to calculate individual variable scores.

The FSI can be used as a tool to assess structural diversity across different types of forests and its temporal development over periods of 10 years. The relationship between structural diversity and species diversity was also established, at least for some of the tested TGs, which shows the possibility of describing the presence / absence of some taxonomic groups using elements of structural diversity in forests. Diversity of other tested TGs was not correlated with the FSI. It is logical that the FSI cannot describe all tested TGs successfully, because this would require an assumption that all TGs have similar habitat demands, included in the FSI. The TGs that were not correlated to the FSI might have demands for structural elements that are not included in the FSI or were not correlated to the FSI, because some structural variables were positively while others were negatively correlated to the diversity of individual TGs and thereby cancelled each other out.

In this project, the focus was on the diversity of structural elements at the plot- / stand-level. Genetic diversity of tree species or taxonomic groups, as well as diversity at the landscape level, are not included in the FSI but are very important for a comprehensive view on biodiversity (Noss & Cooperrider 1994). For instance, Schall *et al.* (2018) found that a mixture of even-aged ('structurally poor') forests can have positive influences on species diversity at the landscape level (beta-diversity). Therefore, a mixture of structurally rich stands (including different expressions of the applied structural elements in the FSI) and structurally poor stands should be combined in order to maximize the (beta-) diversity of TGs on the local / regional scale. Only structurally diverse stands (including the same high expressions for all variables in the FSI) would reduce the possible diversity of TGs, as some groups prefer e.g. monocultures instead of mixed-species forests ('Habitat Heterogeneity Hypothesis'; Sullivan & Sullivan 2001, Okland 1996, Simpson 1949). The support of open forests on 10% of the state-owned forest area, which is a declared goal of the state of Baden-Württemberg (ForstBW 2013), is mainly implemented by intensified harvests. This is a good example of the influence of harvesting intensity on the diversity of tree species. These strongly harvested areas can provide important and rare habitats for different taxonomic groups (e.g. Michiels 2015, Braunisch & Suchant 2013) as well as for rare shade-intolerant tree species (ForstBW 2013), which underlines the recommendation of different HIs on a regional scale. Compared to the stands before intensive harvests, these special areas do not necessarily show a higher structural diversity or biodiversity, but support the rare and endangered open forest species such as wood grouse (*Tetrao urogallus*), woodland brown (*Lopinga achine*) or hermit beetle (*Osmoderma eremita*) via the provision of special structural elements.

Unseld & Bauhus (2017) showed that harvesting intensities were quite heterogeneous in privately owned forest stands in Baden-Württemberg, leading to different structural qualities at small scales. Especially rare and important structural elements can be provided by small forest stands that have not been harvested for many years. Based on structural elements, the FSI can be used to assess the value of forest stands for nature conservation to create a quantitative basis for the selection of forest stands that should be included in voluntary conservation easements.

To support decision-making processes on upcoming harvests in general (on a large scale / across many sites), this index can also be used but has to be handled with caution; local / regional conditions and characteristics (like protected forest areas, forest that mainly fulfil ecosystem services, forests that are used for protection of soil and water or difficult terrain which makes a timber harvest unprofitable) can differ drastically and have to be considered if maintenance of diversity shall be implemented fully. By calculating the index for sampling plots in protected areas (forest reserves), changes of structural diversity without human interference can be analysed and compared to managed forests, which will provide knowledge on the impacts of harvesting on structural diversity.

5.3 The relationship between FSI and taxonomic groups

Based on the presented results, it is possible to describe the presence / abundance of some of the tested taxonomic groups such as ‘birds’, ‘deadwood fungi’ or ‘bacteria’ by the overall value of the developed structural diversity index.

Variation in the diversity of a number of TGs was not captured by the overall FSI-score, which is not surprising because this would require that several of the tested TGs prefer the same habitat characteristics. Nevertheless, knowledge about the demands for specific structural elements was gained (correlation to applied variables within the FSI), so taxon-specific indices can be developed easily on the basis of the FSI. A further step could be a separation of TGs in taxonomic sub-units to focus on groups with the same habitat demands within a TG; for example the TG of ‘coleoptera’ could be separated into sub-units ‘deadwood beetles’, ‘ground beetles’ or ‘burying beetles’ to increase the level of correlation with the FSI and also to gain knowledge about individual habitat demands.

These results, which are limited to three regions of Germany, can be extrapolated across many sites, using the NFI data of Germany. Therefore, information has to be scaled up from the plot-level (inventory of the GBE) to the forest stand-level within the NFI to work on a more reliable data basis. If the results of this step are positive for individual taxonomic groups, habitat quality and its changes over periods of 10 years, referred to the structural demands of these species, can be analysed without additional costs.

5.4 Recommendations for future research

To analyse the diversity of structural elements in forests, as well as changes over 10 year periods, the FSI can be easily adapted to the NFI database and statements for single states of Germany or large forest types can be produced instantly for upcoming inventories. The influence of harvests on structural diversity should be analysed at least over two inventory periods to capture long-time changes of structural diversity as well as direct changes to assess the impacts comprehensively. Application of the FSI to enterprise-inventory data, including information about different harvesting methods and more precise information about the amounts of harvested timber within individual stands, should be performed to assess impacts of harvests at local and regional levels more precisely, such in the study by Marshall (2000) on biological processes in forest soils and the influences of different harvesting methods.

An improvement of the FSI by including formerly missing variables (e.g. microhabitats, growth on downed deadwood or information on the litter layer) could be achieved in upcoming inventories by using the method described for the calculation of the index. A reduction of the FSI owing to missing variables is also possible, if, for example, inventories of other European Countries do not provide data on all aspects of structural diversity that were applied in the index.

In future studies, information about the presence / absence of different taxonomic groups described by the FSI within the German Biodiversity Exploratories might be scaled up to National Forest Inventory data. This might be challenging, given the sampling method in the German NFI. When the description of habitat demands of different taxonomic groups by the FSI using NFI data is possible, this important information can be used to support biodiversity monitoring and to capture changes in habitat qualities over 10 year periods without additional costs across many sites.

The developed FSI can and should be used to assess the level of structural diversity in different types of forests and if possible, changes over inventory periods to analyse the development of structural elements (field of nature conservation). The FSI can be applied to most inventory methods used in forests, by adjusting threshold values for individual ecosystems to capture the ranges of the variables correctly, if necessary. Impacts of harvests on the structural diversity of forests can be analysed to recommend future harvesting intensities in order to maintain structural diversity to support future political and economic decisions. A third possible application of the FSI is in the field of species monitoring or monitoring of individual taxonomic groups, which can be supported by information on structural elements provided by the FSI or by modified versions of the FSI (including only variables that are correlated to the presence /absence or diversity of single TGs) to describe their occurrence with the highest possible precision. This makes the developed index on the structural diversity of forests an important and flexible tool that can be applied in the above mentioned fields in the future.

5.5 References

Bitterlich W (1948) Die Winkelzählprobe (The Angle-Count Sample Plot). Allgm. Forst-u. Holzwirtz. Ztg., 59: 4-5. In Forestry Abstracts (Vol. 10, p. 2314).

Braunisch V, Suchant R (2013) Aktionsplan Auerhuhn Tetrao urogallus im Schwarzwald: ein integratives Konzept zum Erhalt einer überlebensfähigen Population. Vogelwelt, 134, 29-41.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling estimating abundance of biological populations.

ForstBW (2013) Gesamtkonzeption Waldnaturschutz, Stuttgart. http://www.forstbw.de/uploads/media/504-15_ForstBW_Broschuere_Gesamtkonzeption_Waldnaturschutz_01.pdf; 05.06.2018

Jordan GJ, Ducey MJ, Gove JH (2004) Comparing line-intersect, fixed-area, and point relascope sampling for dead and downed coarse woody material in a managed northern hardwood forest. Canadian Journal of Forest Research, 34(8), 1766-1775.

Kändler G, Cullmann D (2014) Der Wald in Baden-Württemberg. Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Forstliche Versuchs-und Forschungsanstalt Baden-Württemberg, Freiburg.

Köhl M (1996) Assessing and monitoring forest biodiversity in Switzerland and Germany. In EFI Proceedings (No. 6, pp. 95-105).

Lappi J, Bailey RL (1987) Estimation of the diameter increment function or other tree relations using angle-count samples. Forest Science, 33(3), 725-739.

Marshall VG (2000) Impacts of forest harvesting on biological processes in northern forest soils. Forest Ecology and Management, 133(1-2), 43-60.

McElhinny C, Gibbons P, Brack C (2006) An objective and quantitative methodology for constructing an index of stand structural complexity. In: Forest Ecology and Management 235 (1-3), S. 54–71. DOI: 10.1016/j.foreco.2006.07.024.

Meyer P (1999) Totholzuntersuchungen in nordwestdeutschen Naturwäldern: Methodik und erste Ergebnisse. Forstwissenschaftliches Centralblatt vereinigt mit Tharandter Forstliches Jahrbuch, 118(1-6), 167-180.

Noss RF, Cooperrider A (1994) Saving nature's legacy: protecting and restoring biodiversity. Island Press.

Okland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation , 76, 297–310.

Paillet Y, Archaux F, Boulanger V, Debaive N, Fuhr M, Gilg O, Guilbert E (2017) Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and Management, 389, 176-186. Polley H, Kroiher F (2017) Nadelwälder in Deutschland. In Pro Wald, March 2017, S. 4-7.

Polley H (2010) Monitoring in Wäldern: Die Bundeswaldinventur und Verknüpfungen für Naturschutzfragen. Naturschutzmonitoring in Deutschland. Stand und Perspektiven. Naturschutz und Biologische Vielfalt, 83, 65-78.

Polley H (2005) Die zweite Bundeswaldinventur - BWI^2 - Der Inventurbericht. Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz.

Regnery B, Paillet Y, Couvet D, Kerbiriou C (2013) Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests?. Forest ecology and management, 295, 118-125.

Ritter T, Saborowski J (2012) Point transect sampling of deadwood: a comparison with well-established sampling techniques for the estimation of volume and carbon storage in managed forests. European journal of forest research, 131(6), 1845-1856.

Rondeux J, Sanchez C (2010) Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: Deadwood. Environmental monitoring and assessment, 164(1-4), 617-630.

Rondeux J (1999) Forest inventories and biodiversity. Unasylva, 50(196), 35-41.

Sabatini FM, Burrascano S, Lombardi F, Chirici G, Blasi C (2015) An index of structural complexity for Apennine beech forests. In: iForest 8 (3), S. 314–323. DOI: 10.3832/ifor1160-008.

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Buscot F (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology.

Simpson EH (1949) Measurement of diversity. Nature, 163, 688.

Sterba H (2008) Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. In: Forestry 81 (5), S. 587–597. DOI: 10.1093/forestry/cpn010.

Sullivan TP, Sullivan DS (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology, 38, 1234–1252.

Tabaku V (2000) Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und-Wirtschaftswäldern. Cuvillier Verlag.

Tomppo E (1996) Biodiversity monitoring in Finnish forest inventories. In Assessment of Biodiversity for Improved Forest Management. Proceedings of the International Workshop, 12-17 June 1995, Koli, Finland/Ed. Bachmann P, Kuusela K and Uuttera J(eds.). FI.

Unseld R, Bauhus J (2017) Verbundvorhaben: KLEN Kleinprivatwald – Energieholz-versorgung und regionale Wertschöpfung. http://www.fnr-server.de/ftp/pdf/berichte/22001715.pdf; 05.06.2018

Vuidot A, Paillet Y, Archaux F, Gosselin F (2011) Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation, 144(1), 441-450.

Chapter 2:

Chapter 2 supporting information I Sampling design of NFI in Germany; Elements and methods of data sampling applied in NFI_{2002} and NFI_{2012} of Germany; *: sampling of deadwood pieces with a diameter of 20 cm in NFI_{2002} was reduced to 10 cm in NFI_{2012}; further information can be found at https://www.bundeswaldinventur.de.

Element	**Sampled via**
Trees with a diameter at breast height (DBH) ≥ 7 cm	Angle count sampling, counting factor 4
Regeneration (20 – 50 cm height)	Fixed radius of 1 m
Regeneration (≥ 50 cm height and < 7 cm DBH)	Fixed radius of 2 m
Deadwood (changes of sampling criteria between NFI_{2002} and NFI_{2012} – calculations refer to NFI_{2002} -method)*	Fixed radius of 5 m

Chapter 2 supporting information II Transformation of variables into scores (between 0 and 1) based on variable-values of NFI_{2002} and literature; '-': threshold values from literature not available or (needed)

Index-variable	**Min NFI_{2002}**	**Max NFI_{2002}**	**Max literature**	**Max applied**
DBHq	0	126.5	80	80
DBH sd	0	69.6	-	70
Height sd	0	24.1	-	25
Species richness (SR)	0	8	-	8
SR_Regeneration	0	8	-	8
Bark-Diversity	0	10	-	10
Flower-Diversity	0	8	-	8
Vol40	0	1854	800	800
Deadwood st mDBH	0	120	80	80
Deadwood d mDM	0	96	80	80
N Decay Classes	0	4	-	4

Chapter 2 supporting information III Comprehensive list of variables derived from NFI_{2002} and NFI_{2012}; N = 52

Aspect	Variable	Description
BD	Bark diversity*	diversity of bark types (based on tree species and DBH)
CH	NC	classification of naturalness (5 classes)
CH	Gini-Simpson-Index DBH	Gini-Simpson index for DBH
CH	Shannon-Index ≥ 7cm DBH	Shannon index for trees ≥ 7 cm DBH
CH	SR ≥ 7cm DBH	species richness of trees ≥ 7 cm DBH
CH	Evenness DBH ≥ 7 cm	tree species evenness (Shannon-Index) for trees ≥ 7 cm DBH
DC	DW CWDI	coarse woody debris index (CWDI) based on volume ha^{-1} per decay class; sampled ≥ 20 cm small diameter
DC	DW N DC	number of decay classes in downed deadwood
DW	DW Types	number of deadwood types (e.g. downed (complete stem or part of the stem), standing (complete stem or part of the stem, stumps, etc.)
DW	DW Vol / ha	volume of all deadwood (standing and downed) per hectare
DW_D	DW INDEX*	deadwood index; calculated like CWDI, including volume ha^{-1} per decay classes and per type of deadwood
DW_D	DW l DBH	downed deadwood mean diameter
DW_D	DW l dm sd	standard deviation of diameter of downed deadwood
DW_D	DW l N / ha	number of downed deadwood pieces per hectare
DW_D	DW l Vol / ha	volume of downed deadwood per hectare
DW_D	VarD DW l	coefficient of variance of diameter of downed deadwood
DW_S	DW st DBH	mean DBH of standing deadwood
DW_S	DW st dm sd	standard deviation of DBH of standing deadwood
DW_S	DW st N / ha	number of standing deadwood snags per hectare
DW_S	DW st Vol / ha	volume of standing deadwood per hectare
DW_S	VarD DW st	coefficient of variance of DBH of standing deadwood
FD	Fruit and Flowers*	availability of different seeds, fruits, pollen (based on species and DBH)
GS	Age	stand age, missing for uneven-aged forests
GS	Basal area / ha	basal area per hectare
GS	Biomass / ha	above ground biomass per hectare
GS	DBHq	quadratic mean diameter at breast height of stands
GS	Growing stock / ha	volume per hectare
GS	Height	mean stand height
GS	N / ha	number of trees per hectare
LLT	VolBigTrees ≥ 40 cm DBH	volume per hectare of tress ≥ 40 cm DBH
LLT	VolBigTrees ≥ 60 cm DBH	volume per hectare of tress ≥ 60 cm DBH
LLT	VolBigTrees ≥ 80 cm DBH	volume per hectare of tress ≥ 80 cm DBH
REG	Cover ratio reg	Percent cover of regeneration
REG	N forest relevant species	number of forest relevant species (NFI classification)
REG	Shannon-Index < 7cm DBH	Shannon index for tree regeneration complete (regeneration 1 and 2)
REG	Shannon-Index Reg 1	Shannon index for regeneration 1 (20 - 50 cm height)

REG	Shannon-Index Reg 2	Shannon index for regeneration 2 (≥ 50 cm height and DBH ≤ 7 cm)
REG	SR < 7cm DBH	species richness of regeneration complete (regeneration 1 and 2)
REG	SR Reg1	species richness of regeneration 1 (20 - 50 cm height)
REG	SR Reg2	species richness of regeneration 2 (≥ 50 cm height and DBH ≤ 7 cm)
REG	Evenness DBH ≤ 7 cm	tree species evenness (Shannon-Index) for trees ≤ 7 cm DBH
REG	Evenness Reg 2	tree species evenness (Shannon-Index) for regeneration 2 (≥ 50 cm height and DBH ≤ 7 cm)
UA	Age sd	standard deviation of stand age
UA	Basal area / ha sd	standard deviation of basal area per hectare
UA	DBH sd	standard deviation of quadratic mean diameter at breast height of stands
UA	N DCl	number of tree diameter classes (class width 10 cm)
UA	VarAge	coefficient of variance of tree age
UA	VarBa/ha	coefficient of variance of basal area per hectare
UA	VarD	coefficient of variance of mean tree diameter
VH	Height sd	standard deviation of stand height
VH	N HCl	number of tree height classes (class width 2 m)
VH	VarH	coefficient of variance of average tree height

*: Calculation of ‘Bark diversity’ and ’Flower diversity’ is performed according to the following tables:

Tree species	**Bark Type**	**DBH Type 1**	**DBH Type 2**	**DBH Type 3**
Acer pseudoplatanus	scaly	< 20 cm	20 - 40 cm	> 40 cm
Betula spp.	furrowed	< 15 cm	15 - 25 cm	> 25 cm
Populus spp.	furrowed	< 15 cm	15 - 25 cm	> 25 cm
Fagus sylvatica	smooth	omitted	omitted	omitted
Pseudotsuga menziesii	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Quercus spp.	furrowed	< 10 cm	10 - 30 cm	> 30 cm
Sorbus torminalis	scaly	< 15 cm	>15 cm	omitted
Larix decidua	furrowed	< 10 cm	10 - 30 cm	> 30 cm
Alnus spp.	furrowed	< 15 cm	15 - 30 cm	> 30 cm
Fraxinus excelsior	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Acer campestre	scaly	< 20 cm	>20 cm	omitted
Picea abies	scaly	< 20 cm	20 - 40 cm	> 40 cm
Carpinus betulus	smooth	< 30 cm	>30 cm	omitted
Larix kaempferi	furrowed	< 10 cm	10 - 30 cm	> 30 cm
Castanea sativa	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Pinus spp.	scaly	< 15 cm	15 - 30 cm	> 30 cm
Prunus avium	smooth	omitted	omitted	omitted
Tilia spp.	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Populus balsamifera	furrowed	< 15 cm	15 - 25 cm	> 25 cm
Quercus rubra	furrowed	< 20 cm	20 - 40 cm	> 40 cm
Robinia pseudoacacia	furrowed	< 10 cm	10 - 25 cm	> 25 cm
Acer platanoides	scaly	< 15 cm	15 - 35 cm	> 35 cm
Pinus nigra	scaly	< 15 cm	15 - 30 cm	> 30 cm
broadleaf species	?	?	?	?
conifer species	?	?	?	?
Abies alba	scaly	< 20 cm	20 - 40 cm	> 40 cm
Ulmus spp.	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Sorbus spp.	smooth	omitted	omitted	omitted
Salix spp.	furrowed	< 20 cm	20 - 35 cm	> 35 cm
Sorbus domestica	scaly	< 20 cm	20 - 40 cm	> 40 cm
Taxus baccata	scaly	< 20 cm	>20 cm	omitted
Sorbus aria	smooth/scaly	< 20 cm	>20 cm	omitted
Malus sylvestris	scaly	< 20 cm	20 - 40 cm	> 40 cm
Pyrus pyraster	scaly	< 20 cm	20 - 40 cm	> 40 cm

To calculate bark diversity, each living tree is assigned to a bark category and shape. Example for spruce, DBH: 30 cm → ‘Sp_scaly_T2’
Bark diversity at plot level is the number of different types of barks and their shapes

Tree species	Fruct. age	Pollination	Fruit type
Acer pseudoplatanus	30	cross + animal	schizocarpic fruit
Betula spp.	25	cross + wind	wingnut
Populus balsamifera	10	cross + wind	capsule fruit
Fagus sylvatica	60	cross + wind	nut
Pseudotsuga menziesii	25	cross + wind	cone
Quercus spp.	65	cross + wind	nut
Sorbus torminalis	15	cross + animal	apple fruit
Larix decidua	35	cross + wind	cone
Alnus spp.	25	cross + wind	cone
Fraxinus excelsior	40	cross + wind	nut
Acer campestre	40	cross + animal	schizocarpic fruit
Picea abies	55	cross + wind	cone
Carpinus betulus	25	cross + wind	nut
Larix kaempferi	35	cross + wind	cone
Castanea sativa	25	cross + animal	capsule fruit
Pinus spp.	40	cross + wind	cone
Prunus avium	20	cross + wind	drupe
Tilia spp.	40	cross + animal	nut
Populus balsamifera	10	cross + wind	capsule fruit
Quercus rubra	50	cross + wind	nut
Robinia pseudoacacia	20	cross + animal	legume
Acer platanoides	30	cross + animal	schizocarpic fruit
Pinus nigra	40	cross + wind	cone
broadleaf species	0	0	0
conifer species	0	0	0
Abies alba	60	cross + wind	cone
Ulmus spp	35	self	wingnut
Sorbus spp.	10	cross + animal	apple fruit
Salix spp.	15	cross + animal	capsule fruit
Sorbus domestica	10	cross + animal	apple fruit
Taxus baccata	30	wind	cone
Sorbus aria	15	cross + animal	apple fruit
Malus sylvestris	15	cross + animal	apple fruit
Pyrus pyraster	15	cross + animal	apple fruit

Like bark diversity, diversity of fruiting and flowering trees is calculated in a similar way. Based on tree species, tree age, pollination and type of fruit, the number of different types of living and fruiting / flowering trees is aggregated. Example 1: oak, 100 years old → 'Oak_c+w_nut'

Example 2: oak, 20 years old → '0' is not counted because no fruit or flowering possible yet

For each living tree on a sampling plot, bark type and fruiting and flowering was calculated and the sum of all (different) present types on plot level is aggregated.

Chapter 2 supporting information IV Variables, aspects of structural diversity and correlations with other calculated variables of the comprehensive list of structural attributes, derived from NFI_{2002} data for whole Baden-Württemberg (forest type 'BW').

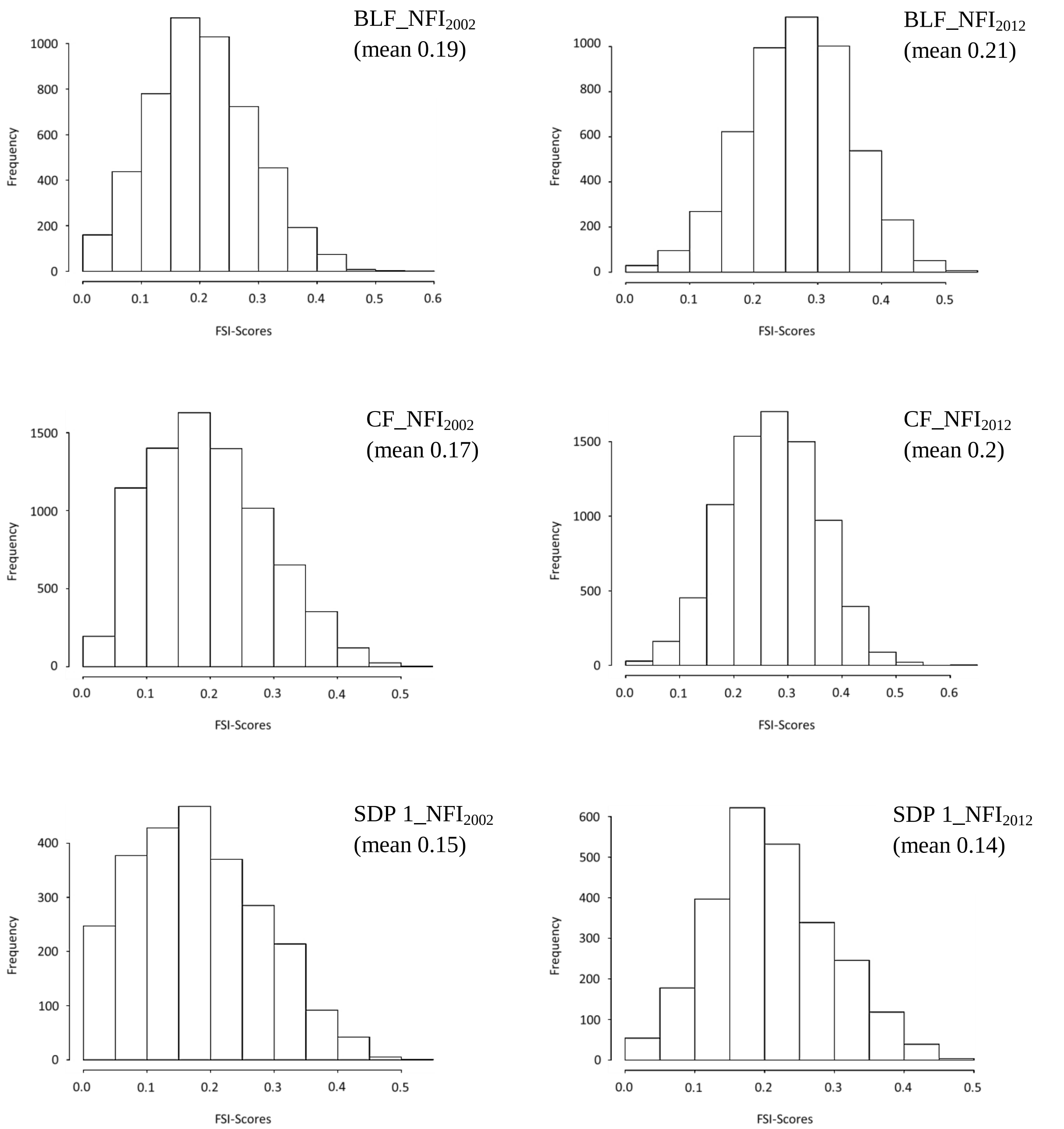
Aspect	**Variable**	**N cor (≥ 0.6)**	**Correlates with**
Growing stock	*DBHq*	7	*volume ha^{-1} of trees DBH > 40 (0.87), mean tree age (0.86), basal area ha^{-1} standard deviation (0.84), basal area ha^{-1} (0.82), DBH standard deviation (0.78), volume ha^{-1} of trees DBH > 60 (0.68), number diameter classes (0.61)*
Uneven-agedness	*DBH sd*	7	*basal area ha^{-1} standard deviation (0.84), DBHq (0.78), variation coefficient DBH (0.77), mean tree age (0.72), number diameter classes (0.7), volume ha^{-1} of trees DBH > 40 (0.67), basal area ha^{-1} (0.61)*
Vertical heterogeneity	*Height sd*	1	*variation coefficient mean tree height (0.93)*
Occurrence of large living trees	*VolTrees40*	9	*basal area ha^{-1} (0.89), DBH (0.87), basal area ha^{-1} standard deviation (0.78), mean tree age (0.77), number diameter classes (0.7), volume ha^{-1} (0.7), biomass ha^{-1} (0.69), DBH standard deviation (0.67), volume ha^{-1} of trees DBH > 60 (0.62)*
Deadwood downed	*DW d mDM*	5	*deadwood number ha^{-1} downed (0.98), deadwood downed volume ha^{-1} (0.97), number deadwood types (0.7), deadwood volume ha^{-1} (0.67), deadwood number decay classes (0.65)*
Deadwood standing	*DW st mDBH*	1	*deadwood number ha^{-1} standing (1)*
Regeneration	*SR Reg*	7	*shannon-index regeneration (0.86), species richness regeneration 2 (0.83), shannon-index regeneration 2 (0.69), variation coefficient DBH (0.69), evenness regeneration 2 (0.68), species richness regeneration 1 (0.65), cover ratio regeneration (0.64)*
Compositional heterogeneity	*SR*	4	*shannon-index DBH ≥ 7cm (0.93), bark (0.84), food (0.78), eveness DBH ≥ 7cm (0.78)*
Decay classes	*N DC*	6	*number deadwood types (0.97), deadwood volume ha^{-1} (0.95), deadwood volume ha^{-1} s (0.74), deadwood downed number ha^{-1} (0.66), deadwood downed volume ha^{-1} (0.66), deadwood downed mean diameter (0.65)*
Bark diversity	*Bark-div.*	4	*species richness (0.84), shannon-index DBH ≥ 7cm (0.76), food (0.67), eveness DBH ≥ 7cm (0.63)*
Diversity of flowering and fruiting trees	*Flower-div.*		*species richness (0.78), shannon-index DBH ≥ 7cm (0.72), bark (0.67), basal area ha^{-1} standard deviation (0.63),), mean tree age (0.63), number diameter classes (0.63), basal area ha^{-1} (0.6), eveness DBH ≥ 7cm (0.6)*

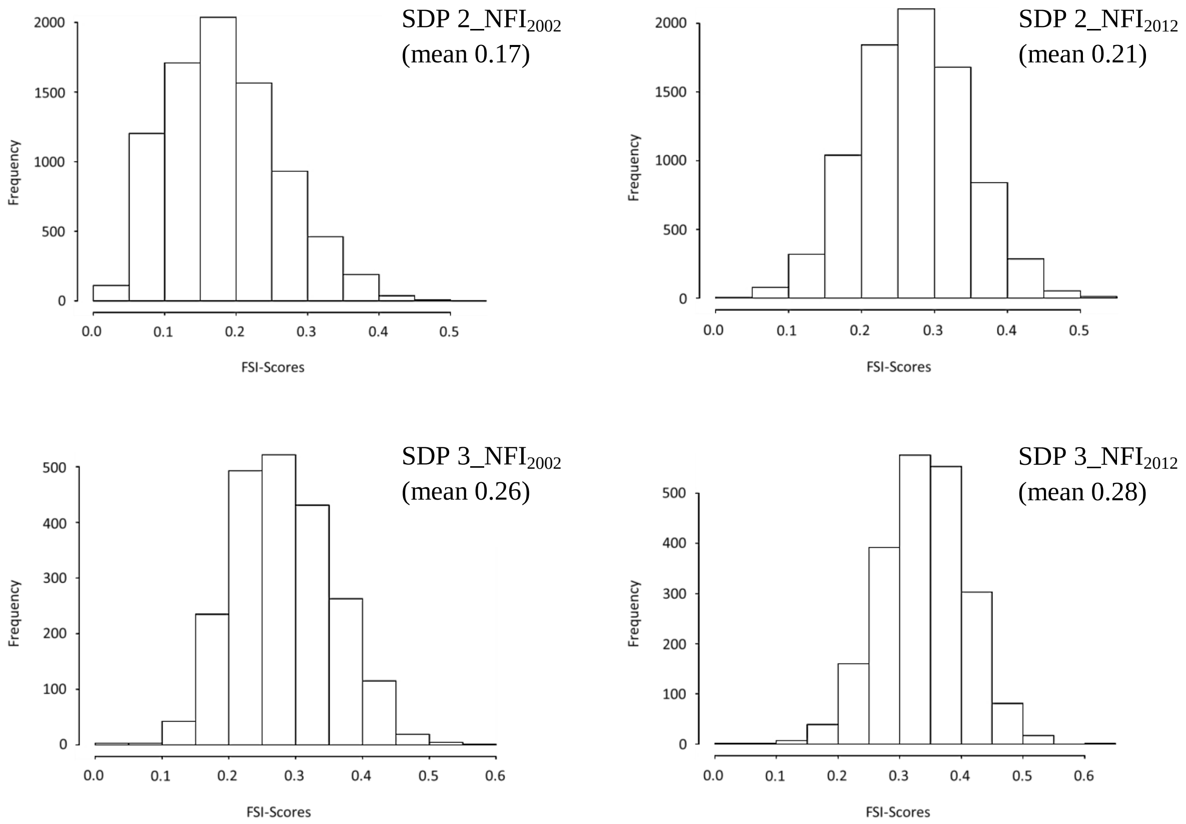
Chapter 2 supporting information V Analysed forest types and corresponding number of sampled plots, distributed over Baden-Württemberg, Germany

Stand type	**Acronym**	**Number of plots**	**Size (ha)**
complete forest of Baden-Württemberg	BW	12.919	1.292.641
broadleaf-dominated stands*	BLF	5.429	543.211
conifer-dominated stands*	CF	7.490	749.429
stand development phase 1* (mean DBH < 20cm)	SDP1	2.529	253.044
stand development phase 2* (mean DBH ≥ 20cm and < 50cm)	SDP2	8.259	826.373
Stand development phase 3* (mean DBH ≥ 50cm)	SDP3	2.131	213.222
broadleaf-dominated stands* + SDP 1*	BLF_SDP1	1.271	127.172
broadleaf-dominated stands* + SDP 2*	BLF_SDP2	3.180	318.182
broadleaf-dominated stands* + SDP 3*	BLF_SDP3	978	97.856
conifer-dominated stands* + SDP 1*	CF_SDP1	1.258	125.872
conifer-dominated stands* + SDP 2*	CF_SDP2	5.079	508.191
conifer-dominated stands* + SDP 3*	CF_SDP3	1.153	115.366
beech-dominated stands* (*Fagus sylvatica* L.)	Be	3.145	314.680
oak-dominated stands* (*Quercus robur* L. + *Qu. petraea* L.)	Oa	930	93.053
spruce-dominated stands* (*Picea abies* L.)	Sp	5.032	503.488
pine-dominated stands* (*Pinus* spp.)	Pi	715	71.540
one-layered stands*	Single	4.357	435.949
two-layered stands*	Double	6.787	679.089
multi-layered stands*	Multi	1.775	177.601
private forest*	Private	4.652	465.466
state forest*	State	3.058	305.975
community forest*	Community	5.151	515.395

* related to NFI classification

Chapter 2 supporting information VI FSI-distribution for a selection of different forest types of Baden-Württemberg for NFI_{2002} and NFI_{2012} (y-axis: frequency of sampling plots; x-axis: FSI-score)




SDP 2_NFI2002
(mean 0.17)
Frequency
FSI-Scores
SDP 2_NFI2012
(mean 0.21)
Frequency
FSI-Scores
SDP 3_NFI2002
(mean 0.26)
Frequency
FSI-Scores
SDP 3_NFI2012
(mean 0.28)
Frequency
FSI-Scores

Chapter 2 supporting information VII Overview of analysed forest types and FSI-scores for NFI_{2002} and NFI_{2012}

Stand type	**FSI_NFI_{2002}**	**FSI_NFI_{2012}**
complete forest of Baden-Württemberg	0.18	0.21
broadleaf-dominated stands*	0.19	0.21
conifer-dominated stands*	0.17	0.2
stand development phase 1* (mean DBH < 20cm)	0.15	0.14
stand development phase 2* (mean DBH ≥ 20cm and < 50cm)	0.17	0.21
Stand development phase 3* (mean DBH ≥ 50cm)	0.26	0.28
broadleaf-dominated stands* + SDP 1*	0.14	0.15
broadleaf-dominated stands* + SDP 2*	0.18	0.22
broadleaf-dominated stands* + SDP 3*	0.25	0.27
conifer-dominated stands* + SDP 1*	0.15	0.14
conifer-dominated stands* + SDP 2*	0.16	0.2
conifer-dominated stands* + SDP 3*	0.26	0.29
beech-dominated stands* *(Fagus sylvatica* L.*)*	0.19	0.21
oak-dominated stands* *(Quercus robur* L. + *Qu. petraea* L.*)*	0.2	0.23
spruce-dominated stands* *(Picea abies* L.*)*	0.16	0.19
pine-dominated stands* *(Pinus* spp.*)*	0.18	0.22
one-layered stands*	0.12	0.14
two-layered stands*	0.18	0.21
multi-layered stands*	0.21	0.24
private forest*	0.17	0.2
state forest*	0.18	0.21
community forest*	0.18	0.21

*: referred to NFI classifications

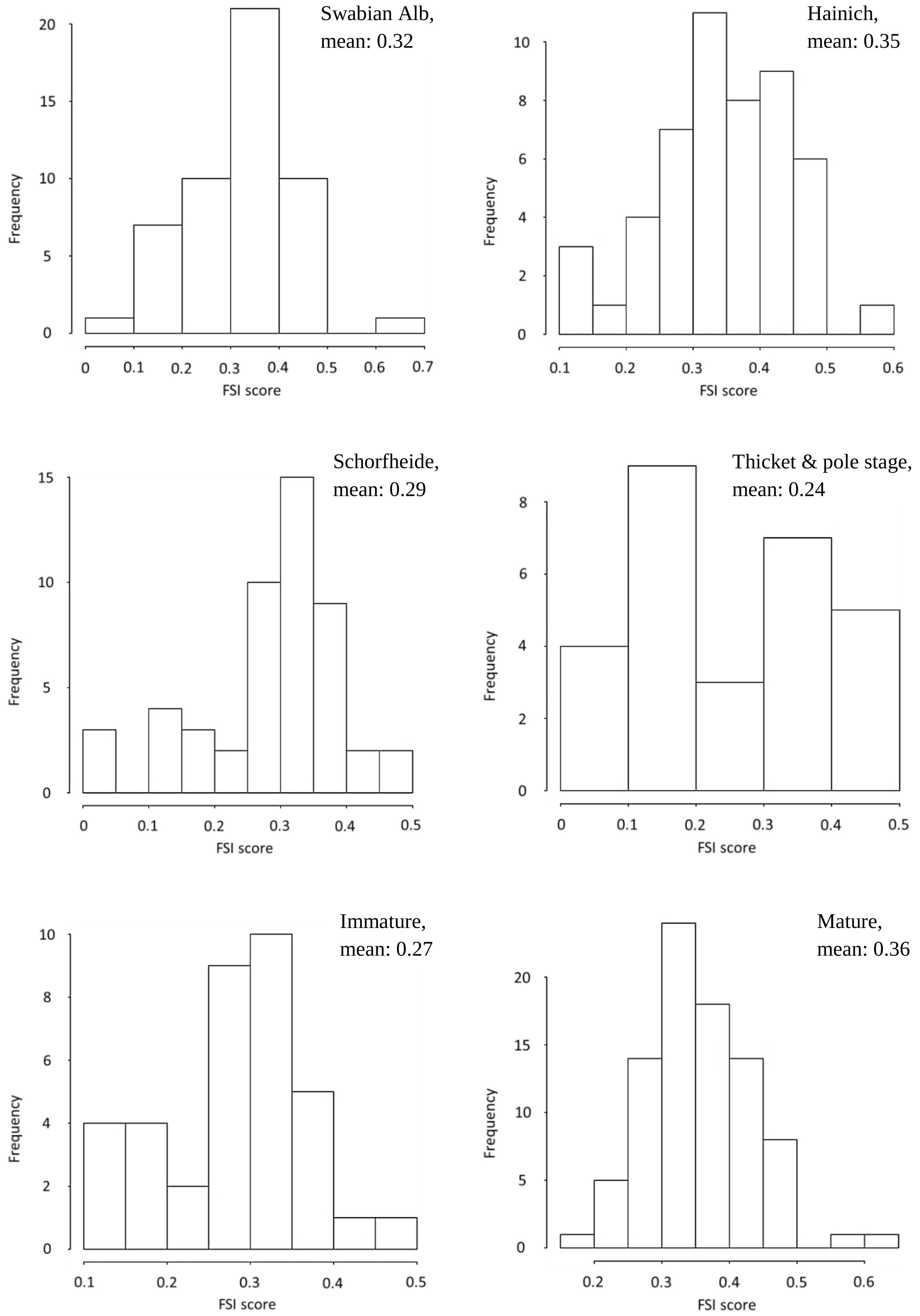
Chapter 3

Chapter 3 supporting information I Aspects and associated variables of structural diversity, included in the FSI (taken from chapter 2). Example calculation on plot level:

Aspect	Variable	Equation	Fictional Example Score	Maximum
Growing stock	DBHq	Score = (X - 0) / (80 - 0)	0.38	1
Uneven-agedness	DBH sd	Score = (X - 0) / (70 - 0)	0.4	1
Occurrence of large living trees	Vol40	Score = (X – 0) / (800 - 0)	0.21	1
Vertical heterogeneity	Height sd	Score = (X - 0) / (25 - 0)	0.5	1
Deadwood downed	DW d mDM	Score = (X - 0) / (80 - 0)	0.36	1
Deadwood standing	DW st mDBH	Score = (X - 0) / (80 - 0)	0	1
Deadwood decay classes	N DC	Score = (X - 4) / (4 - 0)	0.5	1
Regeneration	SR Reg	Score = (X - 0) / (8 - 0)	0.18	1
Compositional heterogeneity	SR	Score = (X - 0) / (8 - 0)	0.22	1
Bark-diversity	Bark	Score = (X - 0) / (10 - 0)	0.25	1
Flower-diversity	Flower	Score = (X - 0) / (8 - 0)	0.3	1
		Sum	3.3	11
		FSI=	3.3 / 11	**= 0.3**

Chapter 3 supporting information II: see chapter 2 supporting information III

Chapter 3 supporting information III Histograms for different types of forests or regions of the German Biodiversity Exploratories



Chapter 3 supporting information IV Mean Index-scores for analysed types of forests of the GBE and equivalent forests types in the NFI-data; lowest and highest FSI-values are highlighted

Region / Forest Type	**FSI mean**	**FSI range**	**NFI_{2012} comparison**	**FSI mean**
All Exploratories	0.32	0.03 – 0.59	Baden-Württemberg	0.21
Hainich	0.35	0.1 – 0.54		
Swabian Alb	0.32	0.07 – 0.59	Baden-Württemberg	0.21
Schorfheide	0.29	0.03 – 0.48		
Pole and thicket	0.24	0.03 – 0.43	SDP1	0.14
Beech unmanaged mature	0.4	0.2 – 0.59		
Broadleaf immature	0.31	0.15 – 0.39	BL_SDP2	0.22
Broadleaf mature	0.37	0.18 – 0.59	BL_SDP3	0.27
Conifer immature	0.24	0.09 – 0.44	CF_SDP2	0.2
Conifer mature	0.34	0.22 – 0.54	CF_SDP3	0.29
Immature	0.27	0.09 – 0.44	SDP2	0.21
Mature	0.36	0.18 – 0.59	SDP3	0.28
Broadleaf-dominated	0.34	0.07 – 0.59	Broadleaf-dominated	0.21
Conifer-dominated	0.26	0.03 – 0.54	Conifer-dominated	0.2

SDP = Stand development phase, BL = Broadleaf-dominated stands, CF = Conifer-dominated stands

Chapter 3 supporting information V Overview of the analysis, selection of taxonomic groups and correlation coefficient of the calculated FSI; empty fields = no sig. correlation, numbers = degree of correlation, confidence level of 0.9 applied

Number of plots	150	50	50	50	112	38	86	36	28
Taxonomic Group	All plots	Swabian Alb	Hainich	Schorf-heide	BL dom	CF dom	mature	im-mature	pole + thicket
Arthropods		0.28							
Bacteria	0.27						0.28	0.38	0.46
Bats						-0.29		-0.49	-0.38
Birds	0.54	0.47	0.37	0.8	0.4	0.73	0.3	0.46	0.57
Bryophytes			0.24	-0.38					
Deadwood fungi	0.38	0.32	0.36	0.52	0.24	0.51	0.22	0.33	0.5
Soil fungi							0.23		
Lichen			0.29						
Small mammals									
Mycorrhiza fungi					0.22				-0.39
Plants									0.59
Vascular plants				-0.25					0.59
Shrubs		0.25	0.39	-0.45	0.32		0.37		0.52
Herbs		-0.25							0.58
Bark beetles			0.27						
Bark beetle antagonists		-0.29	0.43						
Sum of species	0.25				0.28		0.3		0.37
Orthoptera									
Colepotera									
Opiliones						0.3			0.52
Hymenoptera									
Neuroptera		0.41							
Hemiptera		0.32		0.24	0.16				
Araneae	-0.17			-0.4					-0.38
Formicidae	-0.21	0.31		-0.25			-0.21		

Chapter 3 supporting information VI Taxonomic groups and correlation coefficient of the calculated index variables for different types of forests (regions); empty fields = no sig. correlation, numbers = degree of correlation, correlation coefficient 0.9

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
BL_dom	Araneae									-0.21			
CF_dom	Araneae		-0.29	-0.29	-0.34								
Exploratories complete	Araneae	-0.17		-0.28	-0.24					-0.22		-0.14	
Hainich	Araneae			-0.47	-0.43		0.3	0.25		-0.29			
Immature	Araneae		-0.41	-0.41	-0.54								
Mature	Araneae									-0.18			
Pole_thicket	Araneae	-0.38					-0.36	-0.33	-0.38				
Schorfheide	Araneae	-0.40	-0.45	-0.51	-0.32	0.35			-0.27	-0.54	-0.33	-0.3	-0.26
Swabian Alb	Araneae												
BL_dom	Arthropods		0.44	0.33	0.2	-0.2	-0.19	-0.26			0.16		
CF_dom	Arthropods												
Exploratories complete	Arthropods		0.29				-0.14						
Hainich	Arthropods												
Immature	Arthropods		-0.35	-0.35	-0.45								
Mature	Arthropods									-0.22			
Pole_thicket	Arthropods						-0.33						
Schorfheide	Arthropods					0.52		0.31					
Swabian Alb	Arthropods	0.28	0.34							0.37			
BL_dom	Bacteria		-0.29			0.31		0.16					0.16
CF_dom	Bacteria					0.36				0.3			
Exploratories complete	Bacteria	0.27		0.17	0.20	0.26					0.24	0.18	0.26
Hainich	Bacteria						-0.26	-0.28	-0.28				
Immature	Bacteria	0.38	0.50	0.5	0.4	0.36				0.41	0.39		
Mature	Bacteria	0.28	0.19	0.19	0.25	0.31				0.22			0.21
Pole_thicket	Bacteria	0.46		0.39			0.39				0.42	0.38	0.48
Schorfheide	Bacteria		0.25	0.36	0.32								
Swabian Alb	Bacteria										0.25	0.25	
BL_dom	Bark beetles												
CF_dom	Bark beetles								0.31				
Exploratories complete	Bark beetles				-0.17			0.16					
Hainich	Bark beetles	0.27					0.41	0.53	0.45				
Immature	Bark beetles		-0.33	-0.33						-0.33	-0.42	-0.43	-0.38
Mature	Bark beetles				-0.19			0.2	0.2				
Pole_thicket	Bark beetles												
Schorfheide	Bark beetles												
Swabian Alb	Bark beetles												

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
BL_dom	Bats		0.56	0.36		-0.29	-0.24	-0.33		0.33			
CF_dom	Bats	-0.29					-0.28		-0.27	-0.31			
Exploratories complete	Bats		0.38	0.19		-0.23	-0.25	-0.28	-0.19				
Hainich	Bats		0.26	0.3			-0.24			0.34			
Immature	Bats	-0.49	-0.30	-0.3	-0.46		-0.36	-0.33	-0.52		-0.36		
Mature	Bats					-0.36							
Pole_thicket	Bats	-0.38					-0.43	-0.36	-0.48				
Schorfheide	Bats		0.31										
Swabian Alb	Bats												
BL_dom	Birds	0.40	0.38	0.58	0.42					0.33	0.47	0.27	0.29
CF_dom	Birds	0.73	0.64	0.64	0.57		0.45	0.49	0.55	0.47	0.64	0.45	0.69
Exploratories complete	Birds	0.54	0.43	0.55	0.45				0.17	0.39	0.54	0.33	0.44
Hainich	Birds	0.37		0.25		0.24				0.24	0.36		0.3
Immature	Birds	0.46	0.30	0.3						0.34	0.47		0.55
Mature	Birds	0.30	0.28	0.28			0.21	0.2	0.25		0.23		
Pole_thicket	Birds	0.57		0.63	0.62					0.59	0.76	0.59	0.6
Schorfheide	Birds	0.80	0.57	0.6	0.54		0.4	0.3	0.5	0.4	0.78	0.49	0.69
Swabian Alb	Birds	0.47	0.37	0.63	0.55					0.35	0.5	0.47	0.38
BL_dom	Bryophytes					0.23							
CF_dom	Bryophytes												
Exploratories complete	Bryophytes			-0.14		0.22							
Hainich	Bryophytes	0.24				0.44				0.28			0.27
Immature	Bryophytes												
Mature	Bryophytes												0.26
Pole_thicket	Bryophytes												-0.39
Schorfheide	Bryophytes	-0.38	-0.25	-0.26						-0.39	-0.31	-0.3	-0.32
Swabian Alb	Bryophytes		0.30				-0.4	-0.33	-0.32			-0.24	-0.36
BL_dom	Colepotera		0.47	0.36	0.2	-0.21	-0.21	-0.29		0.19			
CF_dom	Colepotera					0.3							
Exploratories complete	Colepotera		0.34				-0.15	-0.14					
Hainich	Colepotera					0.29						-0.24	
Immature	Colepotera		-0.30	-0.3	-0.32							-0.28	
Mature	Colepotera									-0.21			
Pole_thicket	Colepotera						-0.36						
Schorfheide	Colepotera					0.47		0.25					
Swabian Alb	Colepotera		0.32							0.36			
BL_dom	Deadwood fungi	0.24		0.31	0.37						0.3	0.23	0.24
CF_dom	Deadwood fungi	0.51	0.54	0.54	0.51				0.3	0.42	0.31	0.55	0.43
Exploratories complete	Deadwood fungi	0.38	0.19	0.45	0.49						0.39	0.36	0.36
Hainich	Deadwood fungi	0.36			0.31						0.29	0.29	0.42

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
Immature	Deadwood fungi	0.33	0.48	0.48	0.5	0.3						0.3	
Mature	Deadwood fungi	0.22	0.36	0.36	0.32						0.23	0.22	0.3
Pole_thicket	Deadwood fungi	0.50	0.32	0.59	0.68					0.6	0.58	0.6	0.46
Schorfheide	Deadwood fungi	0.52	0.56	0.7	0.6						0.58	0.37	0.47
Swabian Alb	Deadwood fungi	0.32		0.45	0.58						0.33	0.46	
BL_dom	Soil fungi		-0.23	-0.22			0.21	0.24		-0.17			
CF_dom	Soil fungi					0.38							
Exploratories complete	Soil fungi		-0.18	-0.16		0.15		0.18					
Hainich	Soil fungi												
Immature	Soil fungi						-0.29						-0.36
Mature	Soil fungi	0.23				0.28		0.26					
Pole_thicket	Soil fungi		-0.43	-0.37	-0.36					-0.44			
Schorfheide	Soil fungi										-0.24		
Swabian Alb	Soil fungi												
BL_dom	Hemiptera	0.16	0.35	0.22						0.16		0.16	0.16
CF_dom	Hemiptera												
Exploratories complete	Hemiptera		0.26										
Hainich	Hemiptera												
Immature	Hemiptera				-0.38								
Mature	Hemiptera					-0.18							
Pole_thicket	Hemiptera												
Schorfheide	Hemiptera	0.24				0.39		0.31					
Swabian Alb	Hemiptera	0.32	0.36							0.38	0.25	0.24	0.27
BL_dom	Formicidae					-0.22	0.19			-0.17			
CF_dom	Formicidae								-0.27	-0.3			
Exploratories complete	Formicidae	-0.21		-0.19	-0.22	-0.14				-0.25	-0.17		
Hainich	Formicidae		-0.38							-0.4			
Immature	Formicidae		-0.38	-0.38	-0.36				-0.3	-0.39	-0.33		
Mature	Formicidae	-0.21	-0.24	-0.24	-0.2	-0.18				-0.33			-0.2
Pole_thicket	Formicidae												
Schorfheide	Formicidae	-0.25	-0.30	-0.39	-0.28	0.34				-0.32	-0.26		
Swabian Alb	Formicidae	0.31	-0.39				0.57	0.53	0.45	-0.27			0.42
BL_dom	Lichen			-0.19		0.24							
CF_dom	Lichen		-0.28	-0.28									
Exploratories complete	Lichen					0.14							
Hainich	Lichen	0.29	0.25	0.29		0.31	-0.25			0.28		0.32	0.24
Immature	Lichen		0.37	0.37	0.4						0.35		
Mature	Lichen												
Pole_thicket	Lichen		0.34			0.49							
Schorfheide	Lichen												
Swabian Alb	Lichen			0.29	0.31	0.24							

Region / Forest Type	**Taxonomic Group**	**FSI**	**DBH**	**DBH sd**	**Height sd**	**SR Reg**	**SR**	**Bark Div**	**Flower Div**	**Vol 40**	**DW d**	**DW s**	**N DC**
BL_dom	Small mammal		-0.23	-0.2		0.19				-0.35			
CF_dom	Small mammal												
Exploratories complete	Small mammal		-0.17	-0.18	-0.14	0.14				-0.24			
Hainich	Small mammal				-0.3								
Immature	Small mammal											0.28	
Mature	Small mammal		-0.26	-0.26		0.2				-0.3		-0.18	
Pole_thicket	Small mammal												
Schorfheide	Small mammal		-0.28							-0.38			
Swabian Alb	Small mammal												
BL_dom	Mycorrhiza fungi	0.22	0.44	0.42	0.27		-0.25	-0.23		0.35	0.24		
CF_dom	Mycorrhiza fungi												-0.32
Exploratories complete	Mycorrhiza fungi		0.24				-0.19	-0.16	-0.14	0.15			
Hainich	Mycorrhiza fungi			0.27	0.32								0.27
Immature	Mycorrhiza fungi		-0.57	-0.57	-0.33					-0.31		-0.52	-0.42
Mature	Mycorrhiza fungi												
Pole_thicket	Mycorrhiza fungi	-0.39					-0.49	-0.44	-0.39				
Schorfheide	Mycorrhiza fungi										-0.27		-0.42
Swabian Alb	Mycorrhiza fungi		0.48				-0.25			0.37			
BL_dom	Neuroptera			0.26	0.37						0.18		
CF_dom	Neuroptera												
Exploratories complete	Neuroptera				0.21								
Hainich	Neuroptera				0.29								
Immature	Neuroptera												
Mature	Neuroptera						0.21	0.19		-0.28			-0.19
Pole_thicket	Neuroptera		0.54	0.39	0.4								
Schorfheide	Neuroptera							0.3		-0.3			
Swabian Alb	Neuroptera	0.38	0.37	0.42	0.38	0.25				0.29	0.25	0.35	
BL_dom	Hymenoptera		0.18	0.25	0.17		-0.23	-0.18		0.25			
CF_dom	Hymenoptera												
Exploratories complete	Hymenoptera									0.16			
Hainich	Hymenoptera					0.31				0.25			
Immature	Hymenoptera												
Mature	Hymenoptera			0.23									
Pole_thicket	Hymenoptera												
Schorfheide	Hymenoptera												
Swabian Alb	Hymenoptera		0.26							0.27			
BL_dom	Bark beetle antagonists		0.18							0.29			
CF_dom	Bark beetle antagonists						0.32	0.42	0.42				
Exploratories complete	Bark beetle antagonists				-0.15				0.17	0.14	-0.16		

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
Hainich	Bark beetle antagonists	0.43	0.3			0.52		0.28	0.5	0.37			0.28
Immature	Bark beetle antagonists		-0.34				0.28	0.38		-0.28		-0.3	
Mature	Bark beetle antagonists				-0.26				0.21	0.29			
Pole_thicket	Bark beetle antagonists												
Schorfheide	Bark beetle antagonists			-0.24				0.24		0.25			
Swabian Alb	Bark beetle antagonists	-0.29		-0.31	-0.32							-0.38	-0.27
BL_dom	Number herbs		-0.38	-0.24		0.34	0.17	0.2		-0.37			
CF_dom	Number herbs												
Exploratories complete	Number herbs		-0.22	-0.25		0.23		0.17		-0.21			
Hainich	Number herbs												
Immature	Number herbs											-0.31	
Mature	Number herbs		-0.22	-0.22		0.43			-0.19				
Pole_thicket	Number herbs	0.58		0.38	0.43	0.47	0.48	0.37	0.35		0.51	0.46	0.5
Schorfheide	Number herbs					0.3			-0.24	-0.31			
Swabian Alb	Number herbs	-0.25		-0.36						-0.24		-0.33	
BL_dom	Number shrubs	0.32	-0.43			0.48	0.49	0.51	0.38	-0.36	0.22	0.16	0.3
CF_dom	Number shrubs		-0.29	-0.29		0.37							
Exploratories complete	Number shrubs		-0.36	-0.27	-0.16	0.44	0.31	0.39	0.23	-0.30			
Hainich	Number shrubs	0.39				0.48	0.37	0.45	0.4				0.24
Immature	Number shrubs		-0.56	-0.56	-0.41					-0.39		-0.46	
Mature	Number shrubs	0.37				0.61	0.33	0.48	0.33				
Pole_thicket	Number shrubs	0.52				0.49	0.45	0.34			0.41	0.38	0.55
Schorfheide	Number shrubs	-0.45	-0.50	-0.45	-0.28	0.64			-0.36	-0.63	-0.43	-0.24	-0.38
Swabian Alb	Number shrubs	0.25	-0.28				0.44	0.45	0.41		0.24		
BL_dom	Number vascular plants		-0.41	-0.23		0.37	0.25	0.26		-0.39	0.16		
CF_dom	Number vascular plants												
Exploratories complete	Number vascular plants		-0.25	-0.27		0.28	0.18	0.22		-0.24			
Hainich	Number vascular plants					0.28							
Immature	Number vascular plants		-0.33	-0.33								-0.35	
Mature	Number vascular plants		-0.23	-0.23		0.5							
Pole_thicket	Number vascular plants	0.59		0.36	0.38	0.49	0.5	0.39	0.36		0.51	0.45	0.54
Schorfheide	Number vascular plants	-0.25				0.44			-0.29	-0.45			
Swabian Alb	Number vascular plants			-0.37						-0.25		-0.3	

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
BL_dom	Opiliones		-0.32	-0.32			0.31	0.28		-0.43			
CF_dom	Opiliones	0.30	0.32	0.32	0.38	0.27			0.29	0.32			
Exploratories complete	Opiliones		-0.23	-0.22			0.26	0.26	0.17	-0.25			
Hainich	Opiliones		-0.39	-0.43	-0.27		0.39	0.38		-0.38			
Immature	Opiliones				0.44								
Mature	Opiliones												
Pole_thicket	Opiliones	0.52					0.59	0.54	0.53			0.34	0.46
Schorfheide	Opiliones				0.27								
Swabian Alb	Opiliones												
BL_dom	Orthoptera												
CF_dom	Orthoptera												
Exploratories complete	Orthoptera												
Hainich	Orthoptera												
Immature	Orthoptera												
Mature	Orthoptera					-0.19							
Pole_thicket	Orthoptera		-0.37										
Schorfheide	Orthoptera												
Swabian Alb	Orthoptera												0.25
BL_dom	Plants		-0.38	-0.23		0.37	0.23	0.25		-0.32	0.16		
CF_dom	Plants												
Exploratories complete	Plants		-0.23	-0.25		0.29	0.18	0.22		-0.19			
Hainich	Plants					0.25							
Immature	Plants											-0.32	
Mature	Plants		-0.24	-0.24		0.51							
Pole_thicket	Plants	0.59		0.36	0.38	0.42	0.51	0.39	0.37		0.53	0.45	0.55
Schorfheide	Plants					0.41			-0.24	-0.36			
Swabian Alb	Plants			-0.38						-0.24		-0.27	
BL_dom	Sum of species	0.28		0.2	0.19	0.31					0.29		0.25
CF_dom	Sum of species					0.49							
Exploratories complete	Sum of species	0.25		0.18	0.17	0.36				0.16	0.22		0.18
Hainich	Sum of species			0.26						0.24			0.35
Immature	Sum of species					0.44						-0.29	
Mature	Sum of species	0.30	0.21	0.21	0.23	0.35					0.2		0.21
Pole_thicket	Sum of species	0.37		0.32							0.43	0.42	0.47
Schorfheide	Sum of species					0.28							
Swabian Alb	Sum of species		0.38			0.32				0.29	0.33		
BL_dom	Sum of TGs					0.18							
CF_dom	Sum of TGs					0.39							
Exploratories complete	Sum of TGs					0.22							
Hainich	Sum of TGs								0.24				
Immature	Sum of TGs					0.32					0.33		

Region / Forest Type	Taxonomic Group	FSI	DBH	DBH sd	Height sd	SR Reg	SR	Bark Div	Flower Div	Vol 40	DW d	DW s	N DC
Mature	Sum of TGs												
Pole_thicket	Sum of TGs		0.34	0.34	0.37	0.34							
Schorfheide	Sum of TGs		0.30								0.25		
Swabian Alb	Sum of TGs					0.4							-0.37

Chapter 3 supporting information VII Number of forest plots of the Biodiversity Exploratories in different forest types and regions. Some types of forests are only located in Schorfheide, which has to be considered when analysing the data; mixed and pure stands were not distinguished to ensure enough replicates plots per type of forest.

Forest Type	**Swabian Alb**	**Hainich**	**Schorfheide**
Beech immature	11	4	1
Beech mature	7	4	6
Beech pole wood	6	4	0
Beech thicket	9	8	7
Beech selection system	0	13	0
Beech unmanaged mature	5	13	7
Oak immature	0	0	2
Oak mature	0	0	5
Pine / Beech mature	0	0	7
Pine immature	0	0	8
Pine mature	0	0	3
Pine pole wood	0	0	4
Spruce immature	8	3	0
Spruce mature	4	1	0

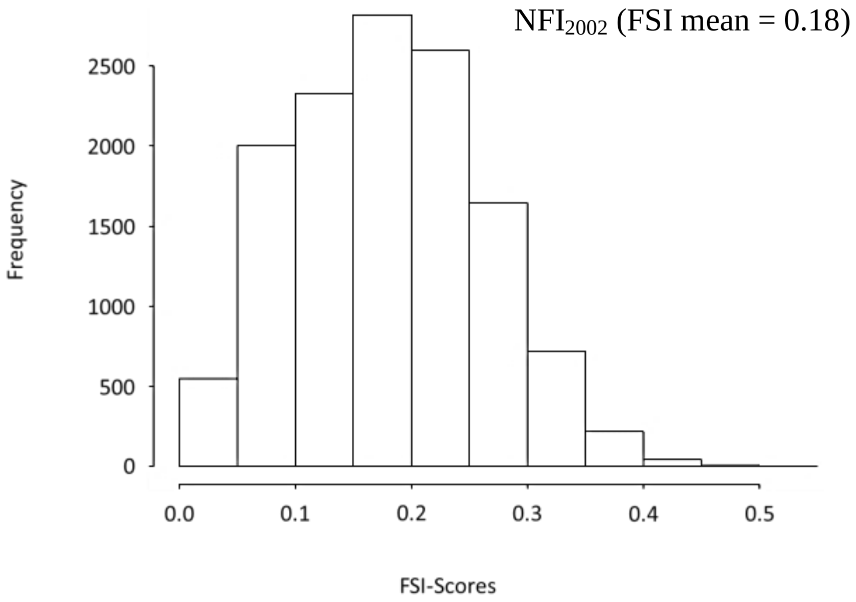
Chapter 3 supporting information VIII Ranges of species richness within individual taxonomic groups that were sampled in the Germany Biodiversity Exploratories and correlated with the FSI

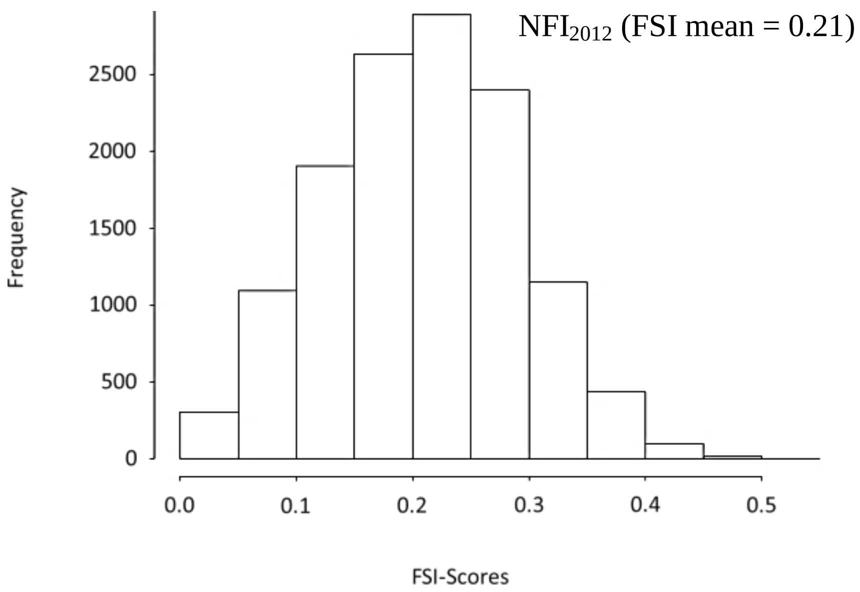
TG	**Min**	**Max**
Arthropods	109	403
Bacteria	323	1084
Microchiroptera	0	11
Aves	15	38
Bryophytes	0	43
Deadwood fungi	21	84
Soil fungi	145	452
Lichen	0	53
Small mammals	0	5
Mycorrhiza fungi	0	318
Plants	1	114
Vascular plants	0	99
Bark beetle antagonists	0	34
Bark beetles	0	20
Species sum	976	1924
Orthoptera	0	7
Coleoptera	94	308
Opiliones	2	12
Neuroptera	1	20
Hemiptera	6	50
Araneae	13	67
Formicidae	0	14
Taxa sum	0.2	0.5
Shrubs	0	16
Herbs	0	91
Hymenoptera	0	41

Chapter 4:

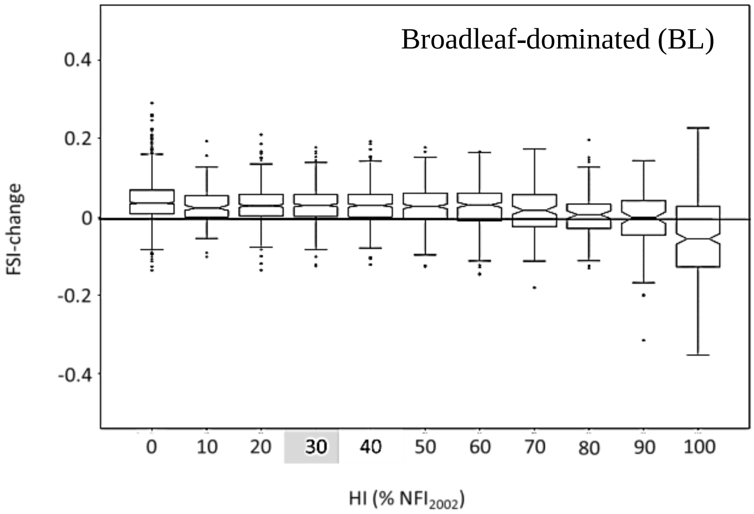
Chapter 4 supporting information I (taken from chapter 2)

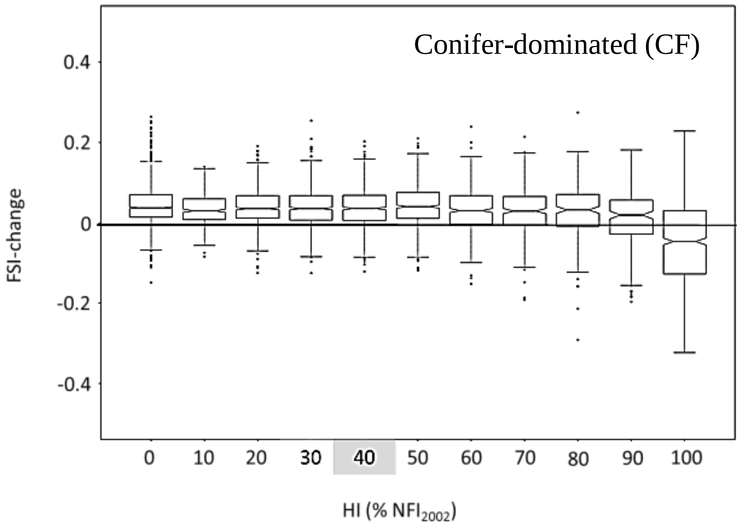
Chapter 4 supporting information II Histograms of FSI distribution for whole forest area of SW-Germany at NFI_{2002} and NFI_{2012} (taken from chapter 2)

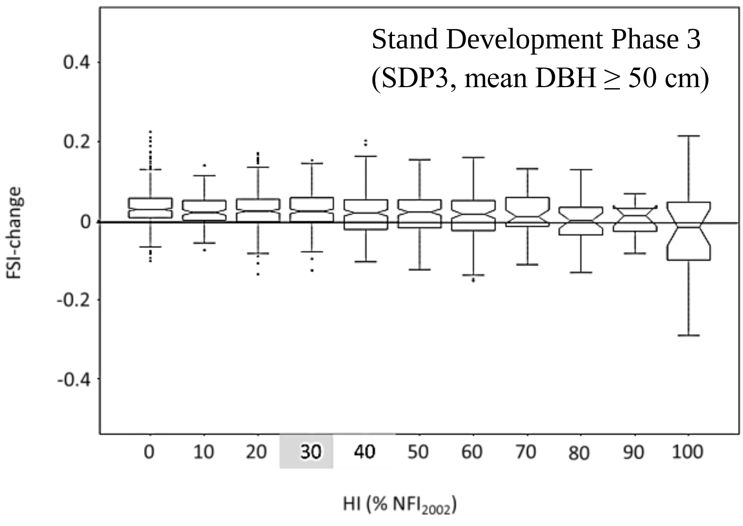


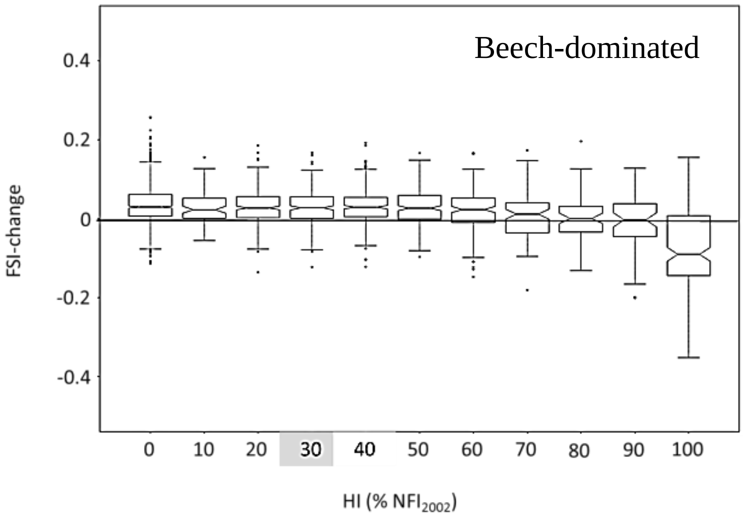


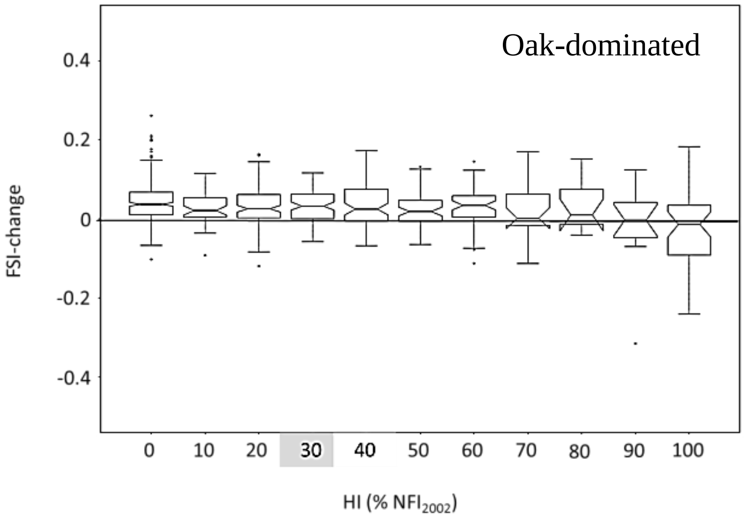
Chapter 4 supporting information III Boxplots for analysed types of forests in SW-Germany illustrating the influences of harvesting intensities (10 %-intervals of standing volume at NFI_{2002}, x-axis) on changes in structural diversity of forests (FSI-Change, y-axis). Black line indicates no change in structural diversity; highlighted number (x-axis) indicates mean harvesting intensity of period 2002 – 2012.

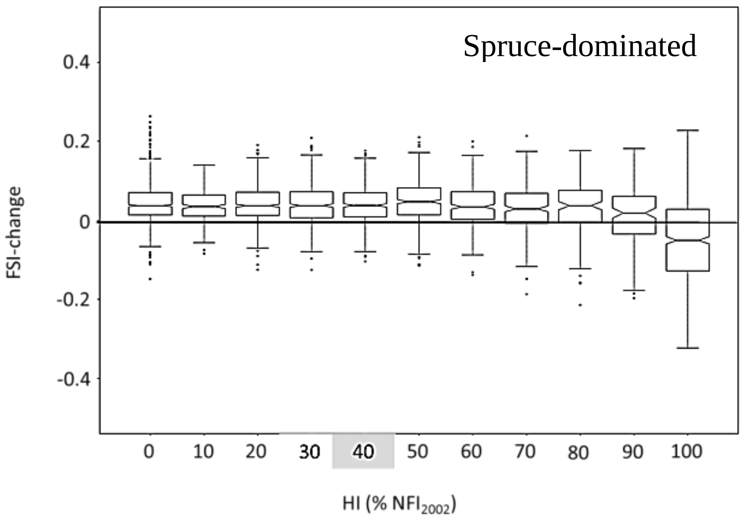


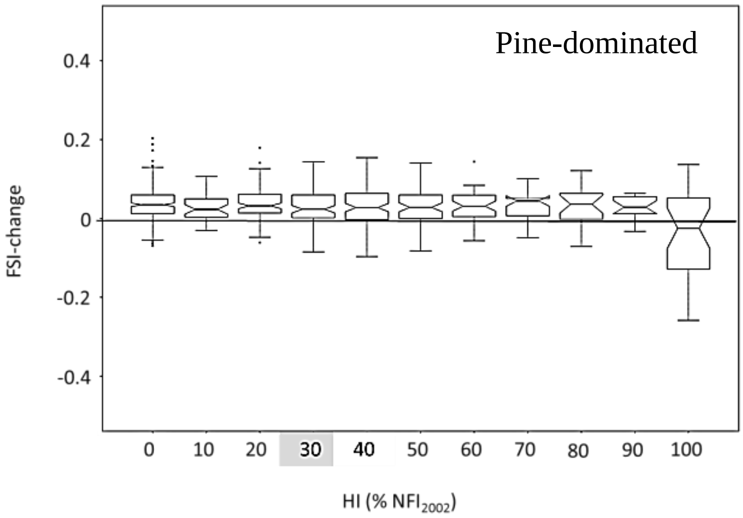


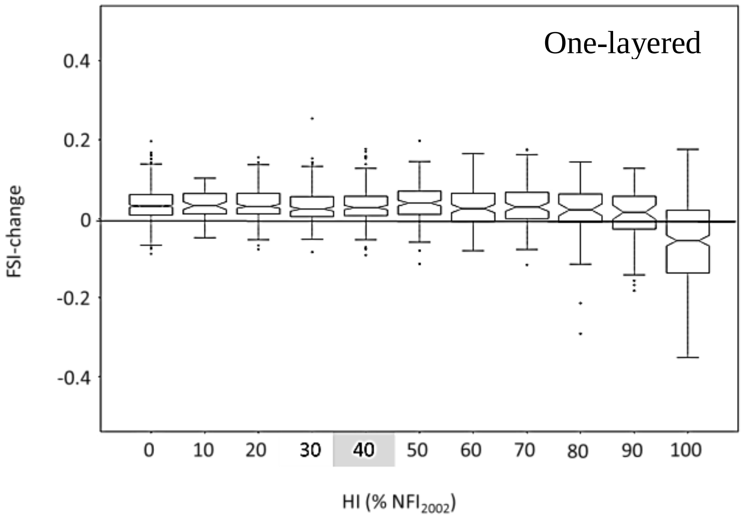


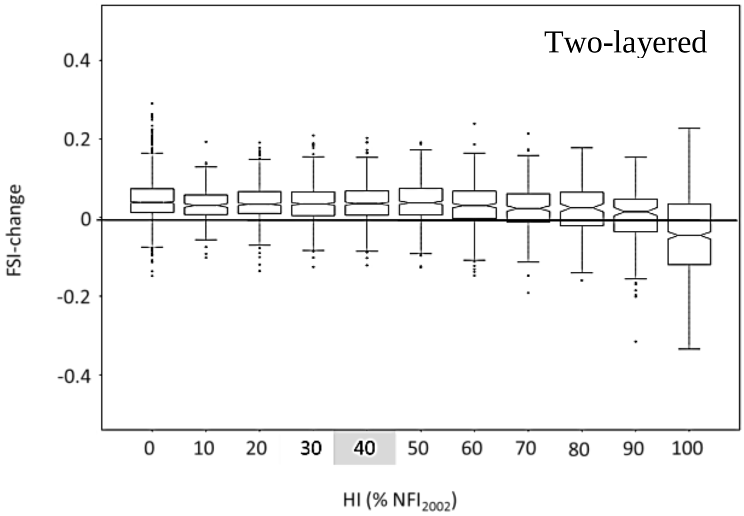

Beech-dominated
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

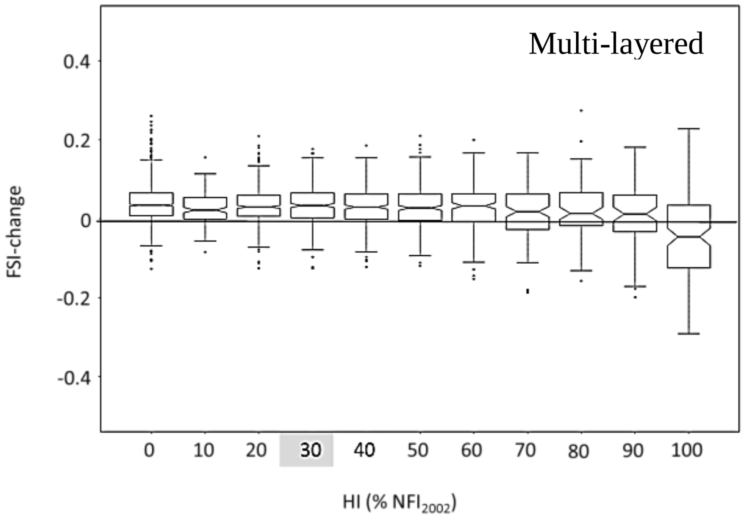

Oak-dominated
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

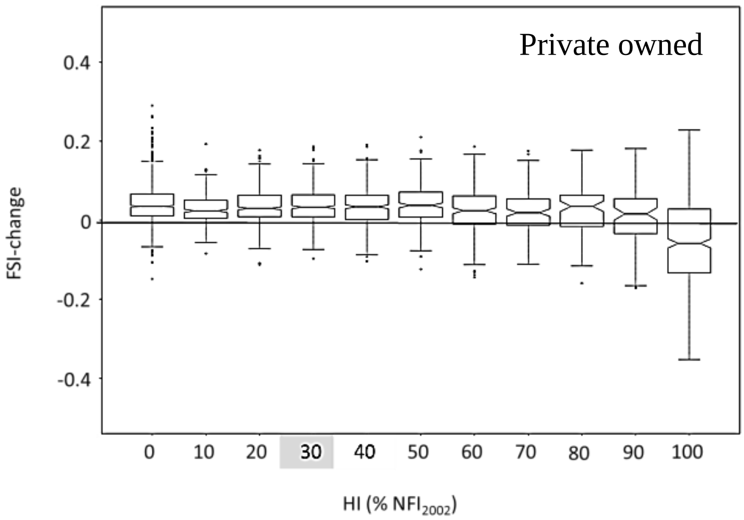

Spruce-dominated
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

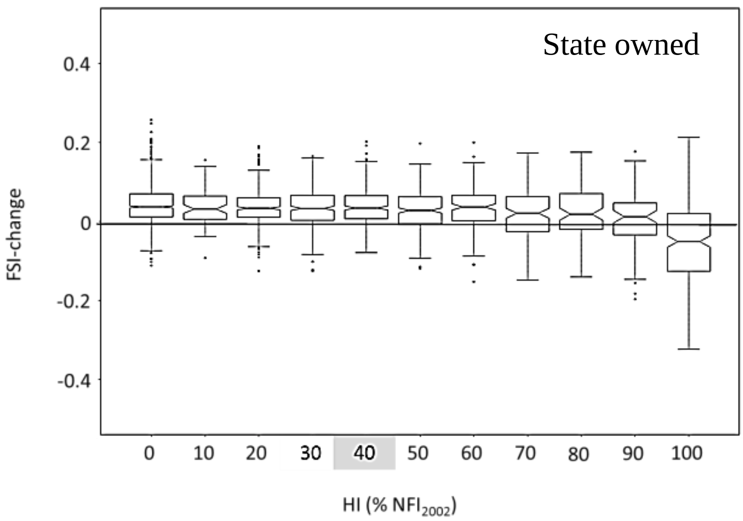

Pine-dominated
FSI-change
0.4
0.2
0
-0.2
-0.4
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

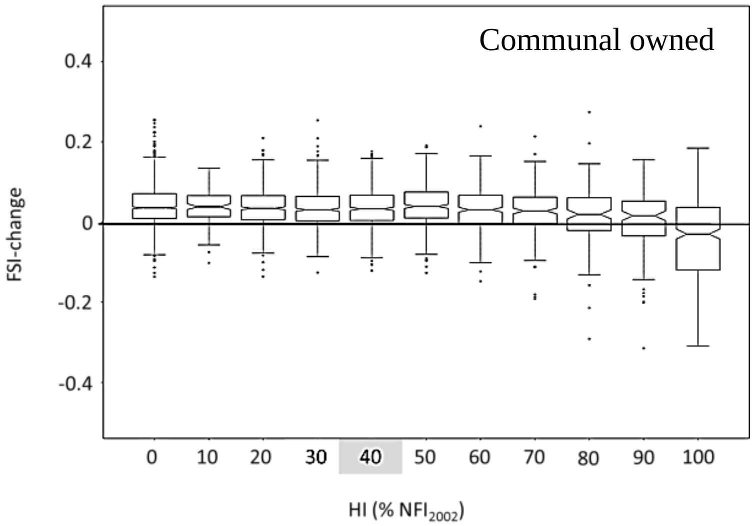

One-layered
FSI-change
0.4
0.2
0
-0.2
-0.4
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)


Two-layered
FSI-change
0.4
0.2
0
-0.2
-0.4
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

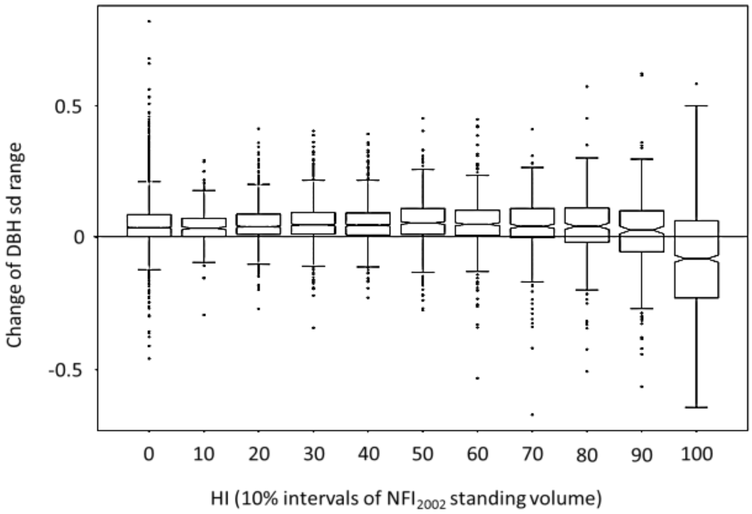

Multi-layered
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI_{2002})


Private owned
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI_{2002})

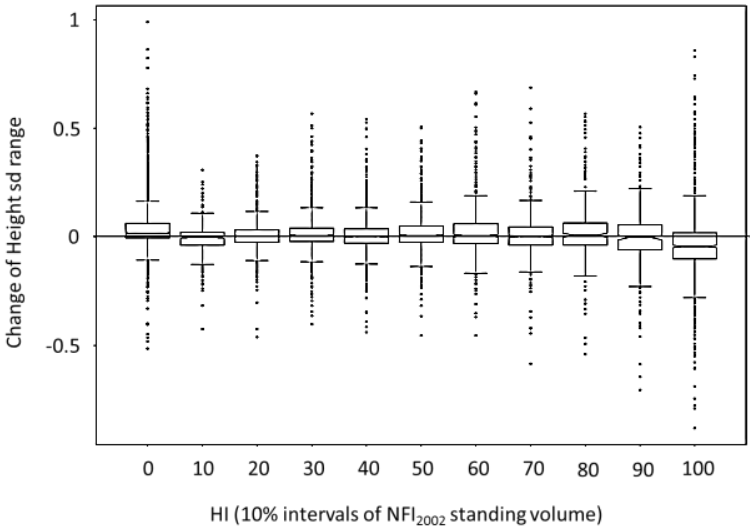

State owned
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI_{2002})


Communal owned
0.4
0.2
0
-0.2
-0.4
FSI-change
0
10
20
30
40
50
60
70
80
90
100
HI (% NFI2002)

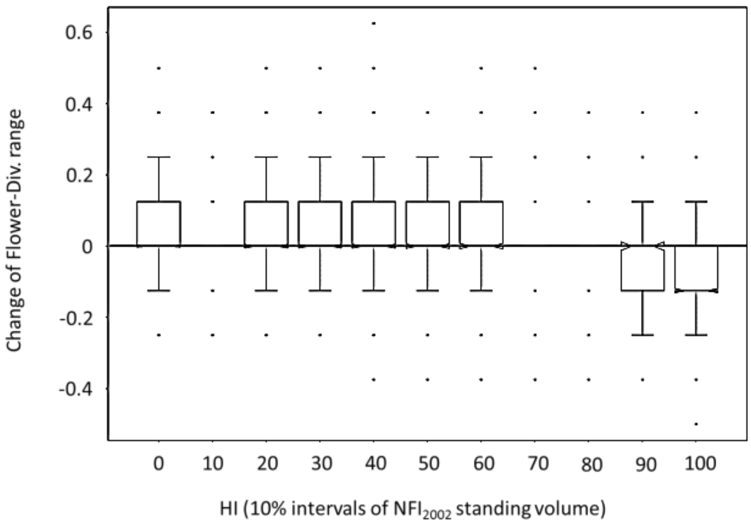
Chapter 4 supporting information IV Changes of individual variable ranges ('variable-range_NFI$_{2012}$' – 'variable-range_NFI$_{2002}$') with increasing HI (HI-classes of 10% referred to NFI$_{2002}$-value) for forests of whole Baden-Württemberg; mean harvesting intensity of 31 % (box '40').



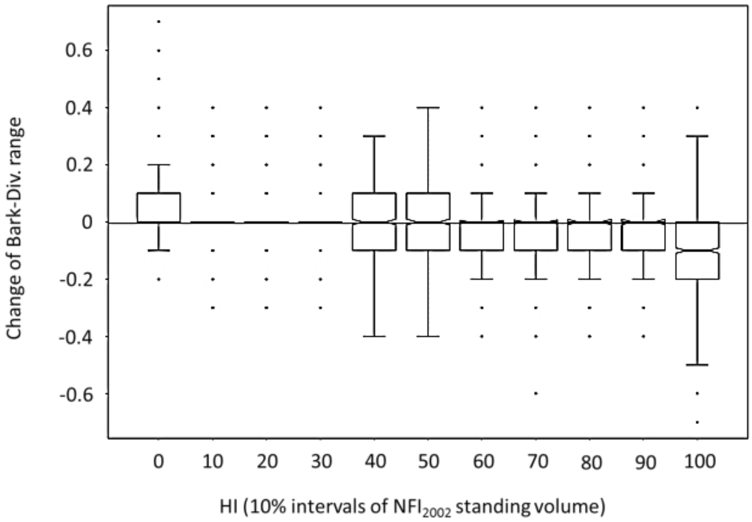
Standard deviation of diameter at breast height (DBH sd)



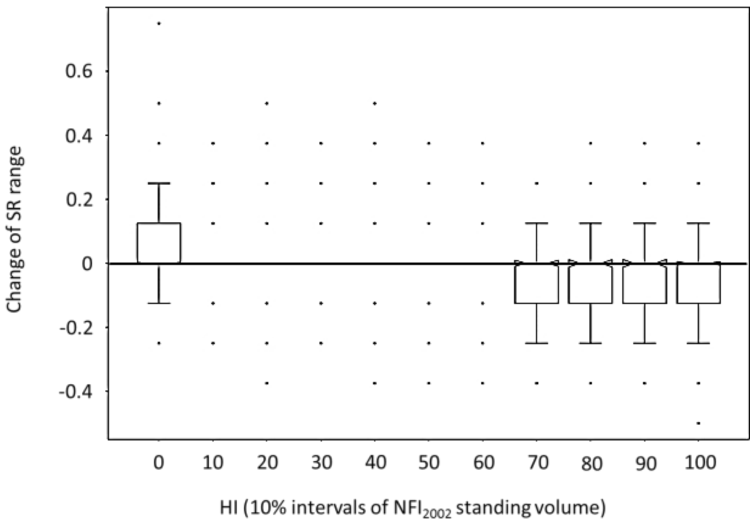
Standard deviation of stand height (Height sd)



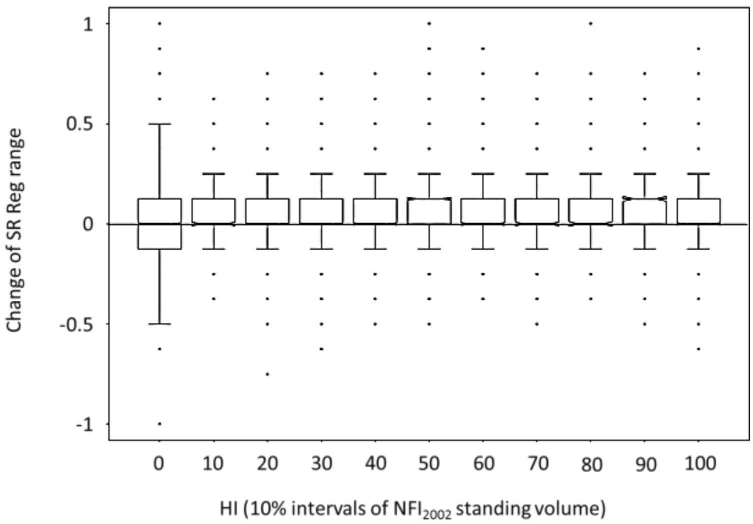
Flower-diversity



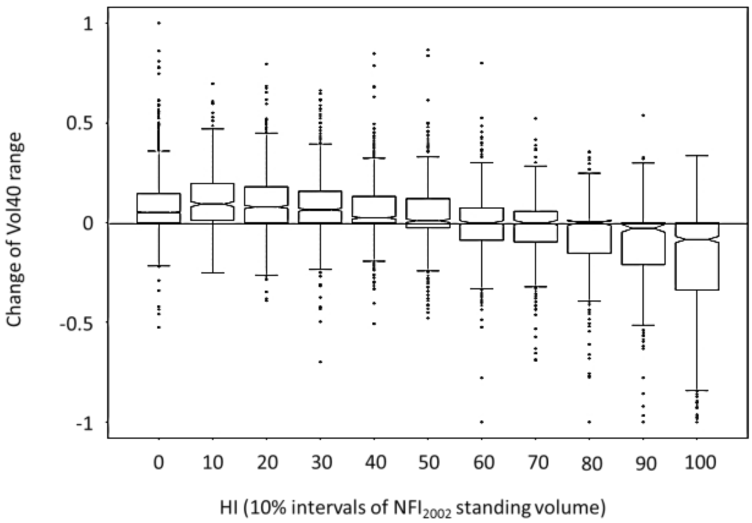
Bark-diversity



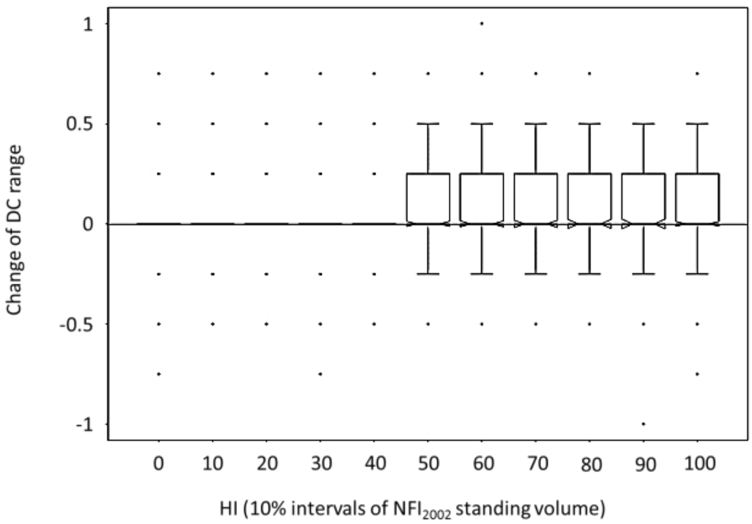
Species richness (SR)



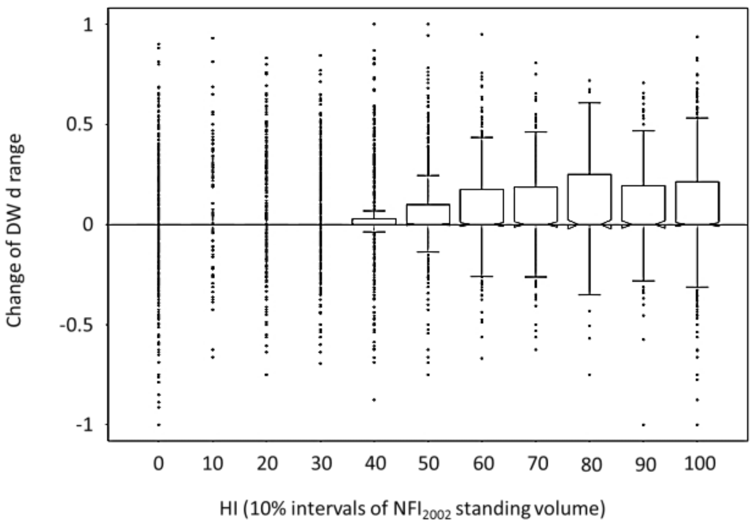
Species richness of the regeneration layer (SR Reg)



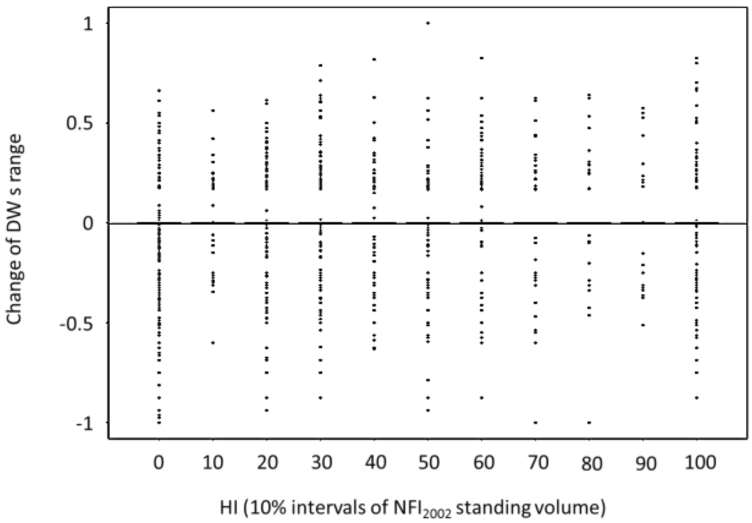
Volume of trees with a DBH ≥ 40 cm (Vol40)



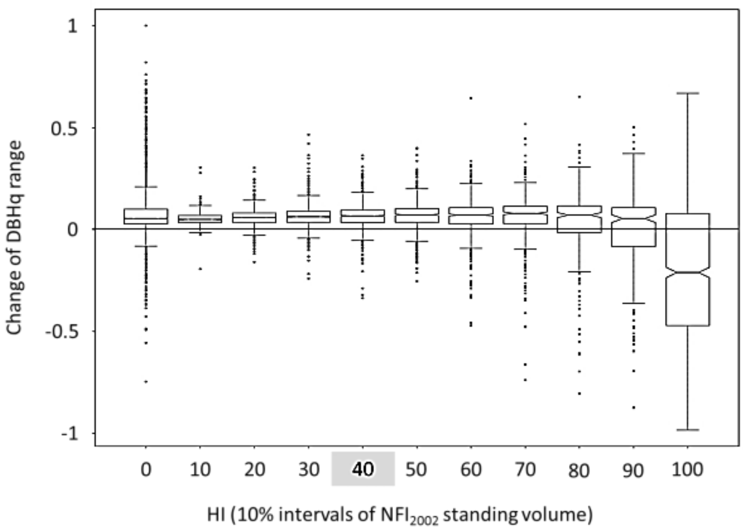
Number of decay classes (DC)



Mean diameter of downed deadwood (DW d)

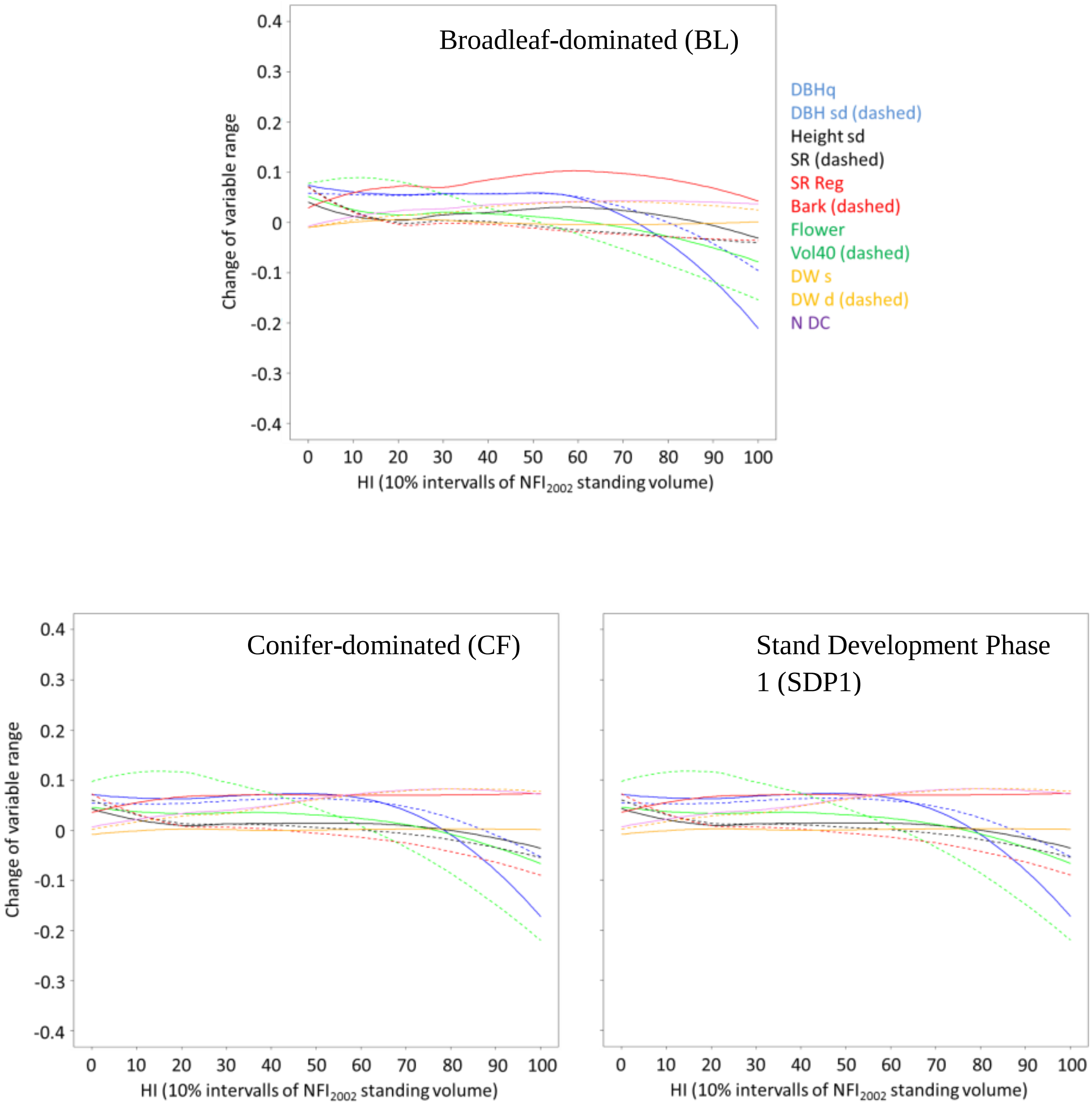


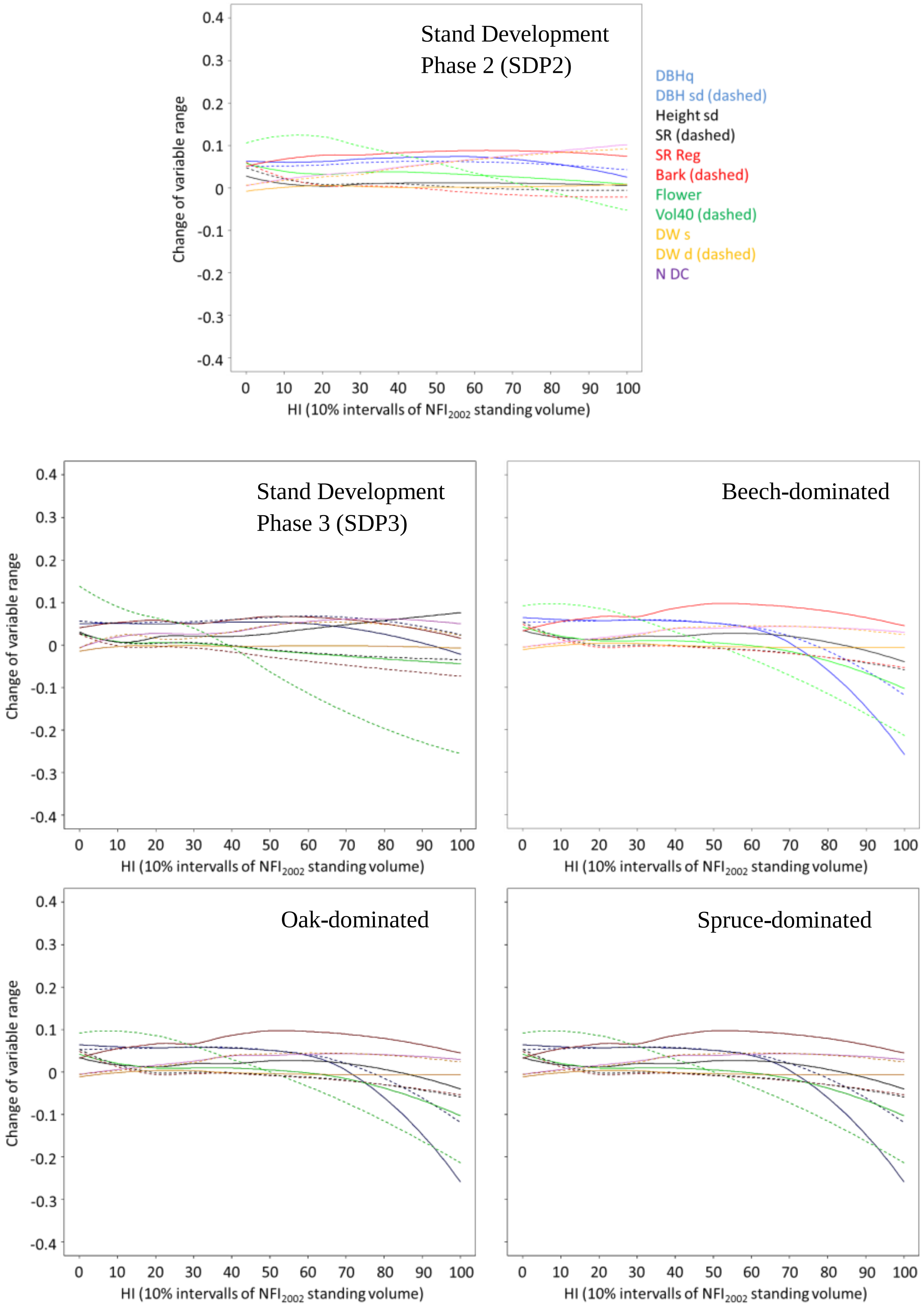
Mean DBH of standing deadwood (DW s)

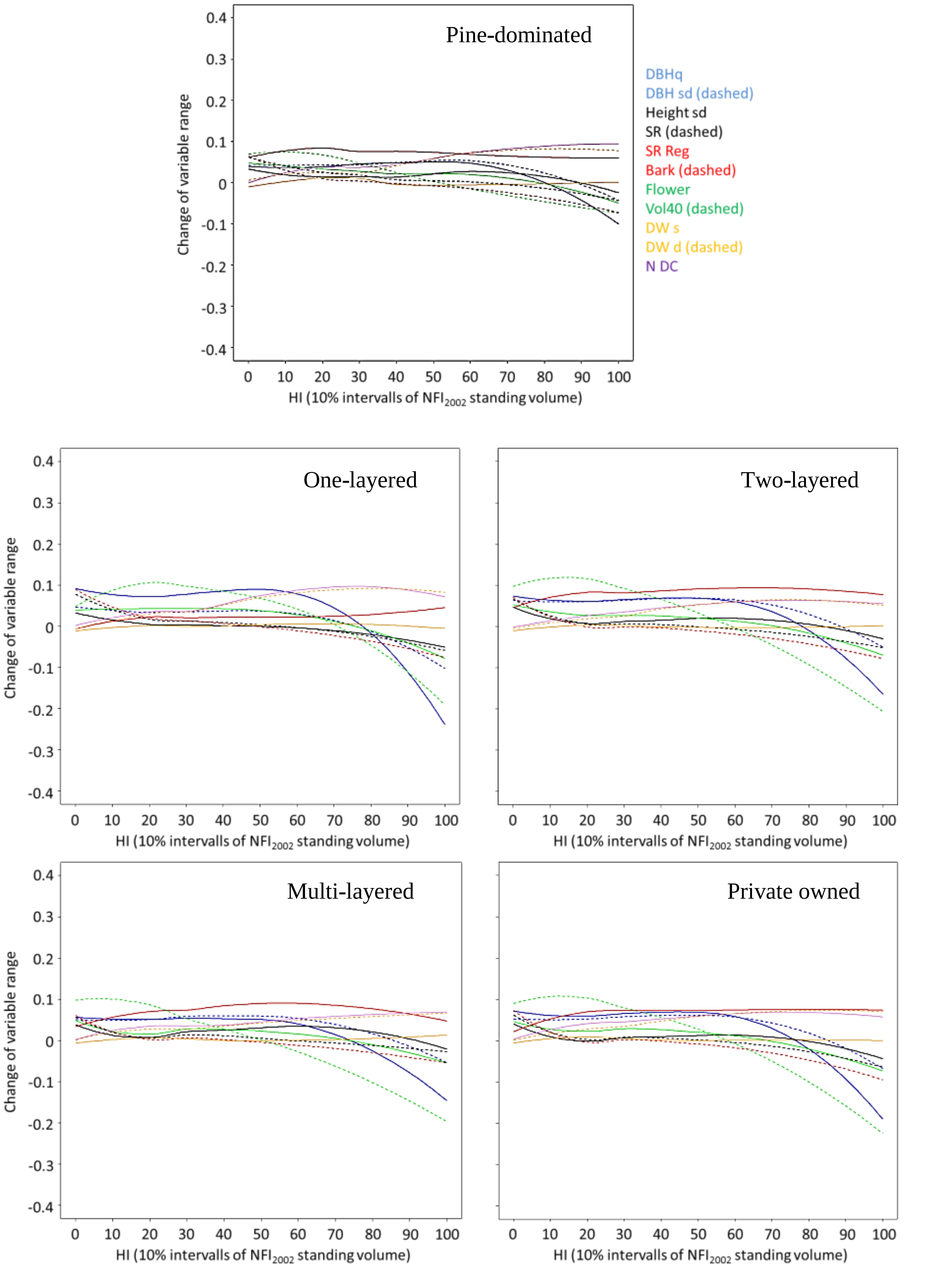


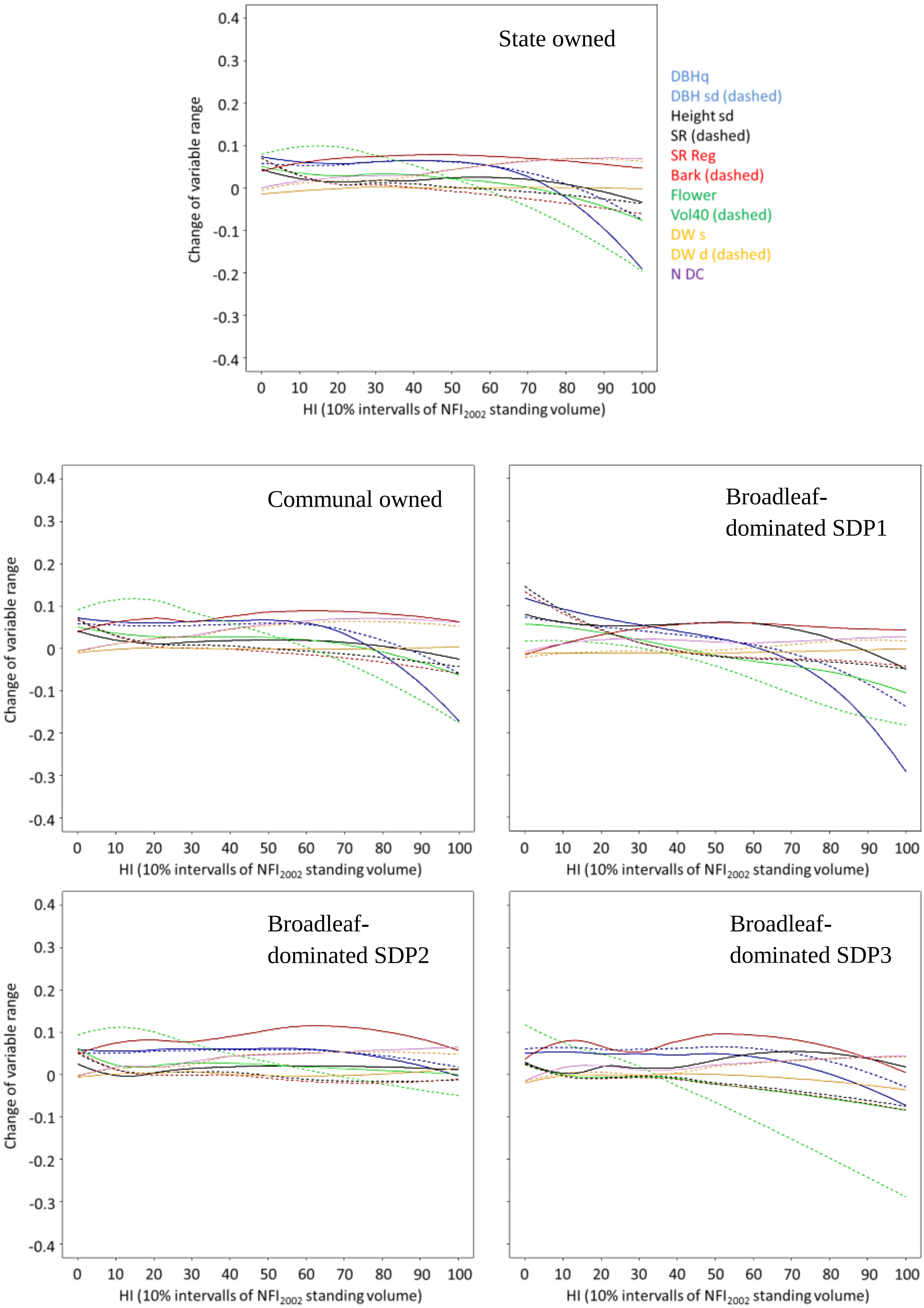
Quadratic mean diameter at breast height (DBHq)

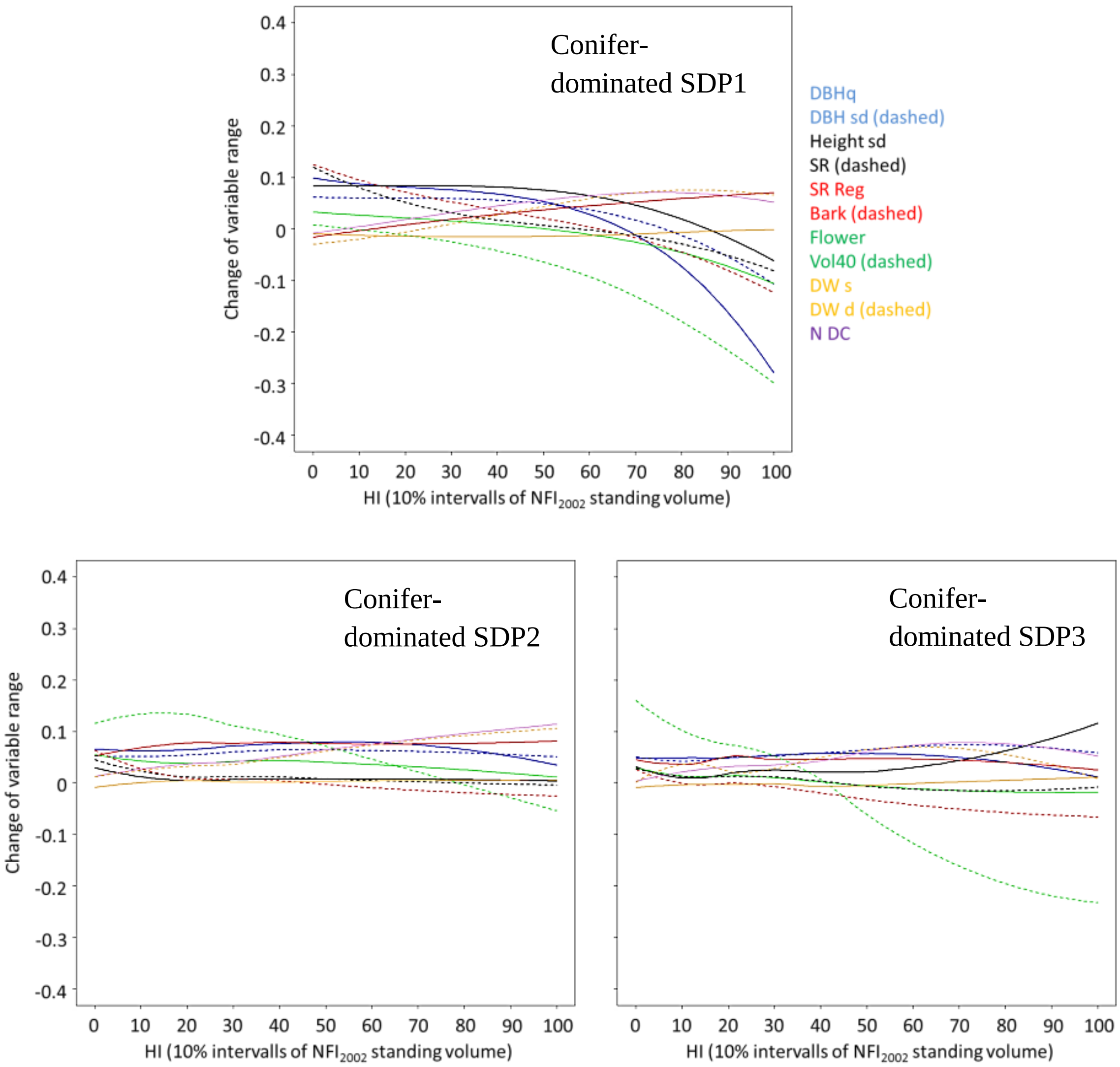
Chapter 4 supporting information V Changes of individual variables applied in the FSI (y-axis: change of variable ranges; x-axis: classes for HI of 10%-intervals (0 – 100%), referred to standing volume at NFI_{2002}), for all analysed types of forests.



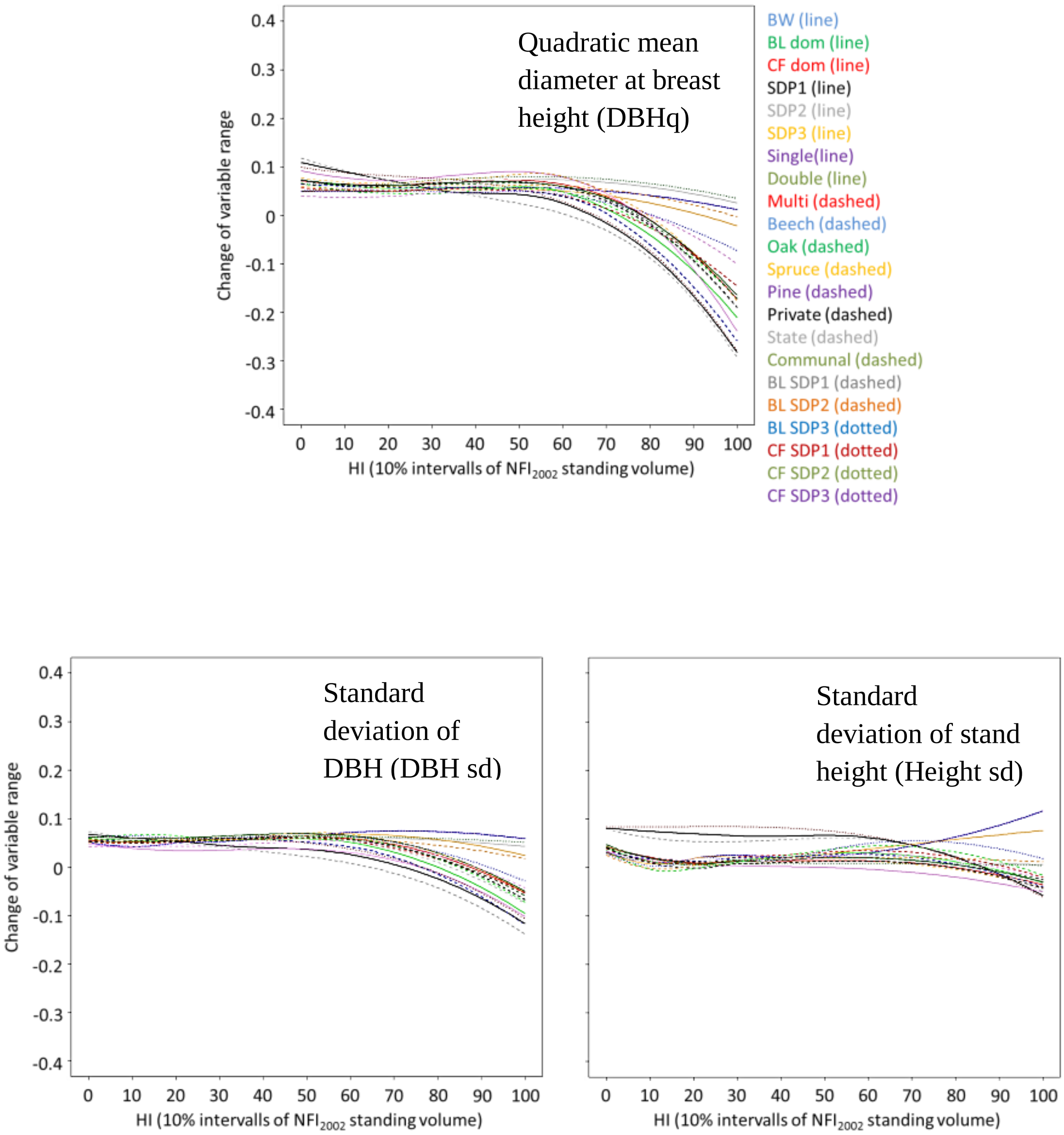

Stand Development Phase 2 (SDP2)
DBHq
DBH sd (dashed)
Height sd
SR (dashed)
SR Reg
Bark (dashed)
Flower
Vol40 (dashed)
DW s
DW d (dashed)
N DC
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)
Stand Development Phase 3 (SDP3)
Beech-dominated
Oak-dominated
Spruce-dominated

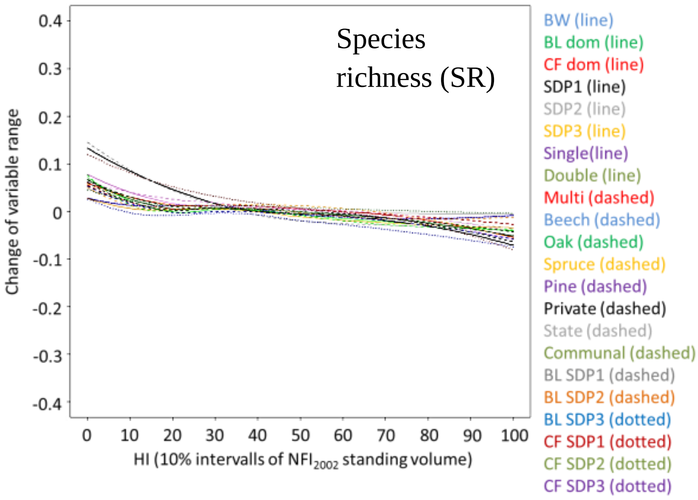

Pine-dominated
One-layered
Two-layered
Multi-layered
Private owned
Change of variable range
HI (10% intervalls of NFI2002 standing volume)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
DBHq
DBH sd (dashed)
Height sd
SR (dashed)
SR Reg
Bark (dashed)
Flower
Vol40 (dashed)
DW s
DW d (dashed)
N DC

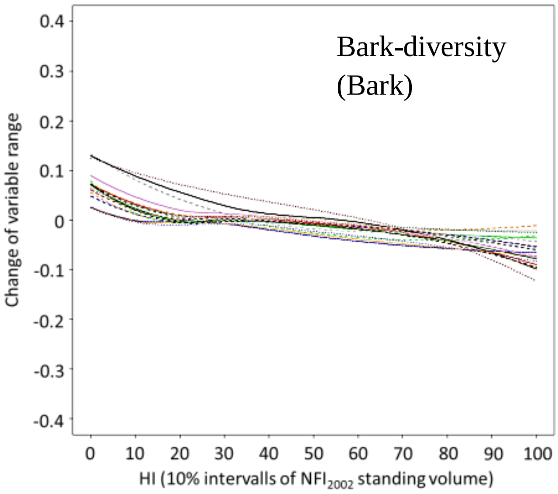

State owned
Communal owned
Broadleaf-dominated SDP1
Broadleaf-dominated SDP2
Broadleaf-dominated SDP3
Change of variable range
HI (10% intervalls of NFI2002 standing volume)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
10
20
30
40
50
60
70
80
90
100
DBHq
DBH sd (dashed)
Height sd
SR (dashed)
SR Reg
Bark (dashed)
Flower
Vol40 (dashed)
DW s
DW d (dashed)
N DC

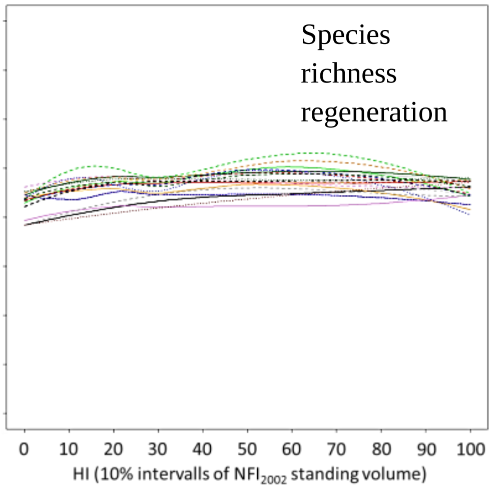

Conifer-dominated SDP1
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)
DBHq
DBH sd (dashed)
Height sd
SR (dashed)
SR Reg
Bark (dashed)
Flower
Vol40 (dashed)
DW s
DW d (dashed)
N DC
Conifer-dominated SDP2
Conifer-dominated SDP3

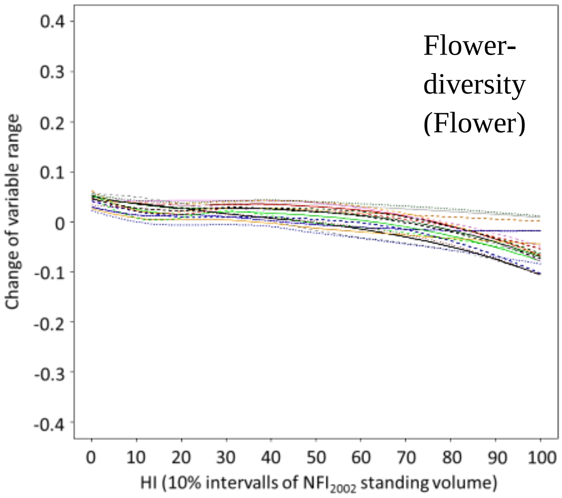
Chapter 4 supporting information VI Changes of applied variables in the FSI with increasing HI for all analysed forest types; x-axis: increasing HI in 10% intervals of NFI_{2002} standing volume; y-axis: change of variable range

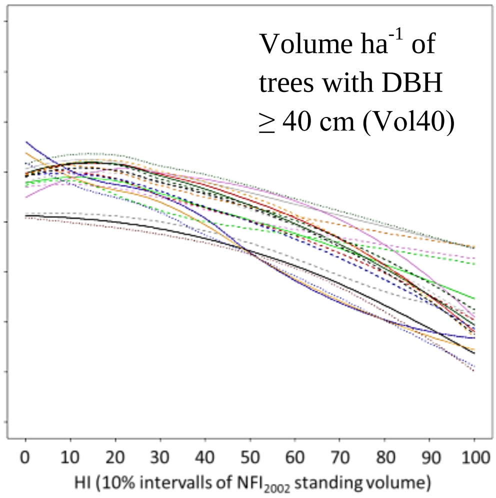


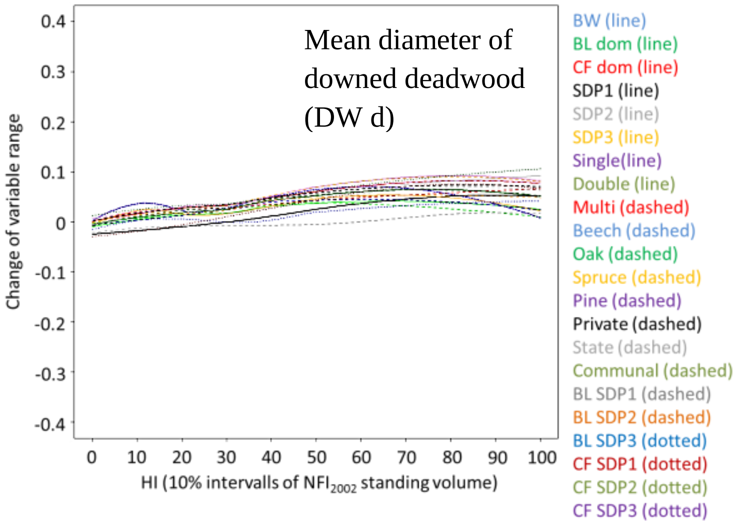

Species richness (SR)
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)
BW (line)
BL dom (line)
CF dom (line)
SDP1 (line)
SDP2 (line)
SDP3 (line)
Single(line)
Double (line)
Multi (dashed)
Beech (dashed)
Oak (dashed)
Spruce (dashed)
Pine (dashed)
Private (dashed)
State (dashed)
Communal (dashed)
BL SDP1 (dashed)
BL SDP2 (dashed)
BL SDP3 (dotted)
CF SDP1 (dotted)
CF SDP2 (dotted)
CF SDP3 (dotted)

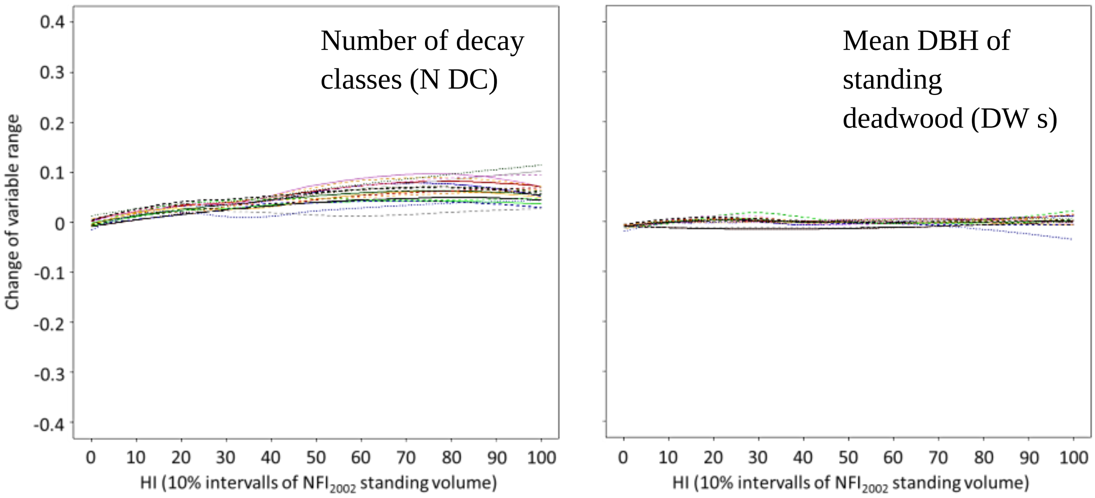

Bark-diversity (Bark)
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)


Species richness regeneration
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)


Flower-diversity (Flower)
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)


Volume ha-1 of trees with DBH ≥ 40 cm (Vol40)
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)


Mean diameter of downed deadwood (DW d)
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)
BW (line)
BL dom (line)
CF dom (line)
SDP1 (line)
SDP2 (line)
SDP3 (line)
Single(line)
Double (line)
Multi (dashed)
Beech (dashed)
Oak (dashed)
Spruce (dashed)
Pine (dashed)
Private (dashed)
State (dashed)
Communal (dashed)
BL SDP1 (dashed)
BL SDP2 (dashed)
BL SDP3 (dotted)
CF SDP1 (dotted)
CF SDP2 (dotted)
CF SDP3 (dotted)


Number of decay classes (N DC)
Mean DBH of standing deadwood (DW s)
Change of variable range
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0 10 20 30 40 50 60 70 80 90 100
HI (10% intervalls of NFI2002 standing volume)
HI (10% intervalls of NFI2002 standing volume)