Eur J Forest Res (2017) 136:739–766
DOI 10.1007/s10342-017-1056-1

ASSMANN REVIEW

Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe

Jochen Dieler[1] · **Enno Uhl**[1] · **Peter Biber**[1] · **Jörg Müller**[2] · **Thomas Rötzer**[1] · **Hans Pretzsch**[1]

Received: 11 July 2016 / Revised: 12 May 2017 / Accepted: 23 May 2017 / Published online: 29 July 2017

Abstract Forests in Central Europe have been used since centuries and were systematically changed by silvicultural practices since the late 1700s. Focusing on possible biodiversity losses, forest stand management primarily impacts on the biodiversity attributes 'composition, structure and functioning' that are interlinked and incorporate different organizational and spatial ecosystem levels. Forest stand management can manipulate tree species diversity, which in turn affects stand structure and finally leads to changes in forest functions and services. We used meta-analyses to review 49 papers with 197 comparisons on compositional and structural diversity between unmanaged and managed forests as well as 53 comparisons of biomass productivity between mixed and monoculture forests throughout the temperate biome of Europe. Besides management impacts, for species and structural comparisons, we took time since abandonment of forest stand management into consideration when dealing with unmanaged forests. For species richness and diversity, we could not detect significant management effects; no significant influences of time since abandonment of management could be identified either. Structural attributes partly revealed considerable responses to forest stand management. Importantly, deadwood quantity, the number of microhabitats, and tree size diversity were reduced by forest stand management, while no effect was found for stand basal area and the number of living trees. Some of these effects become more pronounced with increasing time since abandonment. Forest productivity was significantly enhanced by regular moderate thinning compared with untreated stands and by tree species mixing compared with monospecific stands. Based on these results, we discuss the role of direct and indirect silvicultural effects, interactions between biodiversity components, the problem of defining the unmanaged reference state, and perspectives for forest stand management in practice.

Keywords Forest management · Biodiversity · Composition · Structure · Function · Productivity · Meta-analysis

Introduction

Forests cover of about 31% of the total worldwide land area (FAO 2010). On that account forest ecosystems are a key landscape element for maintaining and conserving biodiversity; a fact that has been rightly underpinned by international and national policies (Convention on Biological Diversity 2010; Forest Europe 2011). Traditionally, many policies on sustaining forest biodiversity have a distinct focus on protected areas. Often, the proportion of protected areas is taken as a key indicator for the success of conservation strategies (Elbakidze et al. 2013). However, creating reserves alone seems not to be sufficient for sustaining biodiversity (Margules and Pressey 2000; Lindenmayer and Franklin 2002). Their efficiency in doing so

---

Communicated by Christian Ammer.

Electronic supplementary material The online version of this article (doi:10.1007/s10342-017-1056-1) contains supplementary material, which is available to authorized users.

✉ Peter Biber
peter.biber@lrz.tum.de

[1] Chair for Forest Growth and Yield, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[2] Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

depends on a variety of factors like size, representativeness, and spatial connectivity (Margules and Pressey 2000; Parviainen et al. 2000; Elbakidze et al. 2013) which cannot be assumed to be given in an optimal configuration. Another, possibly more important reason for the limited contribution of forest reserves to biodiversity preservation is the fact that most of the forest areas (87.5% worldwide according to FAO 2010) are out of protected areas, and there is no sign that this situation will significantly change in future.

Given the so far limited success of policies intended to preserve biodiversity (Butchart et al. 2010), it seems evident that future strategies must absolutely include managed forests (Lindenmayer and Franklin 2002; Parviainen et al. 2000; Wilson et al. 2007). However, knowledge about the effect of management in general on important biodiversity features is often fragmented, major aspects are not yet fully understood, and simplistic concepts do not meet what is required. For instance, a recent synopsis of Europe-wide simulation studies conducted by Biber et al. (2015) shows that higher biodiversity on forest landscape level is not inevitably coupled with less intensive management. Also, natural forests in the temperate zone of Europe would be on large areas dominated by European beech (*Fagus sylvatica* L.) leading to homogenous forest characteristics with comparably low diversity (Hobi et al. 2015).

Biodiversity is considered to simply equate to the 'diversity of life forms' (Hunter 1999, p. 3) which highlights its importance but also its complexity. This all-encompassing wording signifies that ecosystem biodiversity cannot be quantified by a single number. Thus, Noss (1990) suggests to break down biodiversity into the three primary components 'composition', 'structure', and 'function', which are interlinked and incorporate different organizational and spatial ecosystem levels (Fig. 1). As these major components determine a given area's total biodiversity, the concept is appropriate for selecting sets of feasible indicator variables. Since its introduction this concept proved its value in many studies and reviews (Hannah et al. 2002; Hooper et al. 2005; Lindenmayer and Noss 2006) and ecopolitical resolutions (Duelli and Obrist 2003; Larsson 2001). As it is underpinned by indicators of stand composition, structure, and functioning inferable from mostly available forest monitoring and inventory data, it is highly appropriate for being applied in the practice of forest ecosystem management.

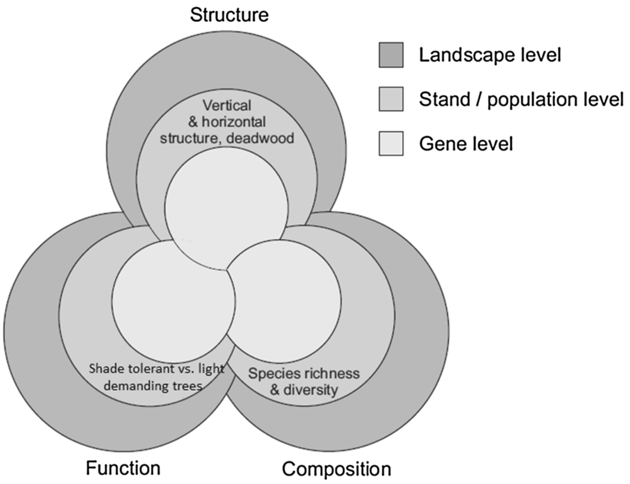

Fig. 1 Relevant components of biodiversity in the context of stand management according to Noss (1990)

This study focuses on the forest stand level (as opposed to the landscape scale), as it is the main operational scale of silviculture. In a given stand, the biodiversity aspect 'composition' is primarily linked to species richness and the floristic and faunistic diversity, while 'structure' links to attributes like the presence or absence of microhabitats or deadwood, and tree size diversity. The term 'function' relates to the number of functionally disparate species, e.g. tree species with different levels of shade tolerance and adaption strategies. At the same time, related indicator variables are, in particular, affected by forest stand management practices (Assmann 1970; Pretzsch 2009) and serve as a starting point for biodiversity preservation in managed forest stands.

The most prominent and visible management action in a given stand is the removal of trees (Schall and Ammer 2013), which immediately changes stand density, structure, and potentially the tree species composition. Besides, the direct choice of tree species when establishing new stands or regenerating mature ones is a highly important silvicultural decision, recently even more so for temperate European forests when it is related to the question of mixed versus monospecific stands (Pretzsch et al. 2015a, b). Despite a multitude of additional possible stand management operations which mostly come along in a greater or smaller extent with any forest stand management (for instance pruning, fertilization, underplanting, skidding trail establishment, pesticide application), we focused this study on these two major silvicultural aspects, tree removal and mixed stand versus monospecific stand establishment.

In the case of tree removal, higher or lower biodiversity, especially in terms of Noss' categories structure and composition, is an outcome of stand management, offering itself to comparisons of managed versus unmanaged stands. The decision to establish mixed stands instead of monospecific ones can be made on very different levels of management intensity. In any case, however, it means an a priori decision for a higher functional (but obviously also compositional and structural) diversity among the trees as the structure-coining organisms in a forest stand. In this context the relevant question for silviculturalists is whether such an a priori chosen level of higher diversity advances or contradicts the fulfilment of other goals, mainly productivity.

Forest stand management in general manipulates structural stand properties like age and size distribution, stand density, tree species composition, stand edges, or vertical layering (cf. Pretzsch 2009). Species variety and abundance in turn are known to interact with the complex structure of forests (McElhinny et al. 2005), which may be more or less affected by silvicultural management measures. This keystone mechanism of preserving biodiversity has been taken up by research asking for sustainable forestry emphasizing biodiversity and nature-oriented forest stand management (Püttmann et al. 2009). Recent studies have approached the dilemma of complexity by focusing on special features of biodiversity like species diversity (Paillet et al. 2010) or even subfeatures such as beetle abundance (Toïgo et al. 2013) and their alteration with thinning activities. On the other hand, the above-mentioned studies as well as studies with a broader focus (e.g. Verschuyl et al. 2011) often entail a generalization of forest biomes or do not differentiate between commercial and natural forests (Burrascano et al. 2013) or between the levels of single stands and forest landscapes. All in all, knowledge about management effects on biodiversity is fragmented due to its complexity and scale dependence.

Focussed on the temperate zone of Europe, this study attempts to consolidate fragmented knowledge about the impact of important stand management measures on forest biodiversity aspects by reviewing existing literature reporting empirical results. We deliberately restrict ourselves to the stand level, which is the main spatial unit of silvicultural operations and follow Noss (1990) in concentrating on the biodiversity components composition, structure, and function. In particular, our research questions are whether managed and unmanaged stands differ in the biodiversity aspects (1) species diversity, and (2) structural diversity. We investigate in addition whether (3) mixed and monospecific stands, representing two distinct stand management decisions for higher and lower functional diversity, are different in terms of stand productivity.

Besides, we discuss how the three biodiversity components might be interlinked and consequences for forest stand management and biodiversity monitoring in the temperate zone of Europe.

Methodology

Selection of relevant literature and data extraction

We reviewed the literature for case studies focusing on the topics of stand structure and species composition that compared biodiversity responses in unmanaged and managed forest stands. Relevant literature was identified by searching the online databases *ISI web of Science* and *Google Scholar* using different combinations of keywords that were: forest stand management, thinning, biodiversity, species richness, species diversity, abundance, structure, structural diversity, managed, unmanaged, natural, virgin, pristine, and forest. In addition, we examined the reference lists of articles found for further publications which were not matched by the database searches.

The initial search was then further refined by biome as we restricted our analyses to temperate forest biomes of Europe. According to McGinley et al. (2011), temperate forests can be classified into five subgroups ranging from Mediterranean forests and dry conifer forests to broadleaved rainforests. In contrast to other biomes, it is characterized by well-defined seasons with a distinct winter, a growing season of 140–200 days during 4–6 frost-free months, air temperatures between -30 to 30 °C and precipitation amounts of 750–1500 mm per year which are comparably evenly distributed throughout the year (McGinley et al. 2011). Our restriction to temperate forests of Central and Western Europe—while keeping in mind that temperate forests also occur in eastern North America and Northeastern Asia—is due to the fact that European forests have an extraordinary long management history and the argument that management effects on biodiversity might depend on this history (Biber et al. 2015). For those cases where no explicit reference to a biome was given, we used the aforementioned definition by McGinley et al. (2011).

In total, we found 49 articles that reported 197 pairwise comparisons of response variables with mean, standard deviation and sample sizes for the reference group of unmanaged forests and the treatment group of forest stand management (Tables 1, 2). If reported, we also registered the time since management had been abandoned in the unmanaged forests in order to test its influence as a moderator variable. In some cases the relevant values had to be extracted from graphs and the standard deviation had to be back-calculated, for instance, from standard error and sample size, respectively. Furthermore, for studies reporting results relevant for the biodiversity categories 'structure' and 'composition', it was necessary to assign the collected results to subcategories, as response variables differed in their ecological meaning.

The list of subcategories for 'structure' comprises response variables expressing (1) stand basal area, (2) number of living trees, (3) mean tree size, maximum tree size related variables (mostly number of large trees), (4) tree size diversity (5) number of microhabitats, and (6) the amount of dead wood. The response variables reported for compositional diversity aspects range from comparably simple measures like the total number of species or mean

Table 1 Data used in the meta-analyses concerning composition

Study	Year	Country	Biodiversity component	Subcategory	Guild	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
1. Paillet et al.	2010	France	Composition	Species diversity	Dictyostelids cellular slime moulds	Abundance	0.126	−2.072	0.313	130.20	102.72	5	16.40	15.94	5	10
2. Winter et al.	2005	Germany	Composition	Species diversity	Mesophilic forest ground beetles	Abundance	0.684	−0.379	0.003	57.00	5.00	3	39.00	2.00	11	50
3. Puratong et al.	2014	Germany	Composition	Species diversity	Operational taxonomic unit (fungi)	Species diversity (H′)	0.826	−0.191	0.005	2.30	0.28	8	1.90	0.28	8	20
4. Laiolo et al.	2004	Italy	Composition	Species diversity	Bird communities	Abundance	0.844	−0.169	0.005	4.50	2.10	166	3.80	1.70	59	30
5. Czeszczewik et al.	2014	Poland	Composition	Species diversity	Bird communities	Species diversity (H′)	0.897	−0.108	0.001	3.90	0.14	8	3.50	0.31	8	93
6. Czeszczewik et al.	2014	Poland	Composition	Species diversity	Bird communities	Species diversity (H′)	0.912	−0.092	0.001	3.40	0.20	8	3.10	0.11	8	93
7. Puratong et al.	2014	Italy	Composition	Species diversity	Operational taxonomic unit (fungi)	Species diversity (H′)	0.957	−0.044	0.004	2.30	0.28	8	2.20	0.28	8	20
8. Erdmann et al.	2006	Poland	Composition	Species diversity	Oribatid mites	Species diversity (H′)	1.000	0.000	0.020	0.80	0.20	4	0.80	0.10	4	
9. Czeszczewik et al.	2014	Poland	Composition	Species diversity	Bird communities	Species diversity (H′)	1.000	0.000	0.001	3.50	0.17	8	3.50	0.24	8	93
10. Durak	2012	Poland	Composition	Species diversity	Plant species (herb layer)	Species diversity (H′)	1.029	0.029	0.001	3.11	0.39	32	3.20	0.24	30	28
11. Durak	2012	Poland	Composition	Species diversity	Plant species (herb layer)	Species diversity (H′)	1.050	0.048	0.001	3.02	0.20	32	3.17	0.34	30	77
12. Durak	2012	Poland	Composition	Species diversity	Plant species (tree layer)	Species diversity (H′)	1.232	0.209	0.037	0.56	0.49	32	0.69	0.43	30	28
13. Durak	2012	Poland	Composition	Species diversity	Plant species (tree layer)	Species diversity (H′)	1.360	0.307	0.026	0.50	0.35	32	0.68	0.38	30	77

Table 1 continued

Study	Year	Country	Biodiversity component	Subcategory	Guild	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
14. Durak	2012	Poland	Composition	Species diversity	Plant species (shrub layer)	Species diversity (H′)	1.508	0.411	0.021	0.59	0.39	32	0.89	0.41	30	28
15. Durak	2012	Poland	Composition	Species diversity	Plant species (shrub layer)	Species diversity (H′)	3.389	1.221	0.097	0.18	0.29	32	0.61	0.42	30	77
16. Paillet et al.	2010	France	Composition	Species richness	Dictyostelids cellular slime moulds	Mean species richness	0.429	−0.847	0.252	2.80	0.83	5	1.20	1.30	5	10
17. Burrascano et al.	2008	Italy	Composition	Species richness	Plant species richness	Number species per plot	0.640	−0.447	0.024	26.10	7.70	9	16.70	5.90	9	100
18. Sitzia et al.	2012	Italy	Composition	Species richness	Tree species	Species richness	0.690	−0.370	0.006	4.20	0.90	10	2.90	0.30	10	55
19. Czeszczewik et al.	2014	Poland	Composition	Species richness	Bird communities	Species richness	0.722	−0.326	0.005	16.90	1.59	8	12.20	2.15	8	93
20. Friedel et al.	2006	Germany	Composition	Species richness	Epiphytic lichens	Mean density of species	0.727	−0.318	0.021	1.10	1.00	100	0.80	0.90	100	52
21. Boch et al.	2013	Germany	Composition	Species richness	Lichens	Mean lichen species richness	0.788	−0.238	0.021	23.10	8.47	7	18.20	8.94	125	20
22. Oheimb et al.	2004	Germany	Composition	Species richness	Lichens	Mean species richness	0.789	−0.236	0.011	3.80	1.50	45	3.00	1.80	45	46
23. Laiolo et al.	2004	Italy	Composition	Species richness	Bird communities	Species richness	0.800	−0.223	0.004	3.50	1.40	166	2.80	1.20	59	30
24. Puratong et al.	2014	Germany	Composition	Species richness	Operational taxonomic unit (fungi)	Species richness	0.806	−0.215	0.005	38.70	5.94	8	31.20	4.24	8	20
25. Czeszczewik et al.	2014	Poland	Composition	Species richness	Bird communities	Species richness	0.825	−0.192	0.003	12.00	1.69	8	9.90	0.83	8	93
26. Friedel et al.	2006	Germany	Composition	Species richness	Epiphytic bryophytes	Mean density of species	0.882	−0.125	0.009	1.70	1.20	100	1.50	0.90	100	52
27. Boch et al.	2013	Germany	Composition	Species richness	Lichen species	Mean lichen species richness	0.894	−0.112	0.007	6.60	3.20	41	5.90	3.26	266	20
28. Boch et al.	2013	Germany	Composition	Species richness	Lichen species	Mean lichen species richness	0.902	−0.103	0.008	5.10	1.85	38	4.60	3.04	103	20

Table 1 continued

Study	Year	Country	Biodiversity component	Subcategory	Guild	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
29. Oheimb et al.	2004	Germany	Composition	Species richness	Bryophytes	Mean species richness	0.909	−0.095	0.004	11.00	4.00	45	10.00	2.50	45	46
30. Winter et al.	2005	Germany	Composition	Species richness	Saproxylic fungi	Species richness	0.925	−0.078	0.009	80.00	13.00	3	74.00	6.00	11	50
31. Puratong et al.	2014	Germany	Composition	Species richness	Operational taxonomic unit (fungi)	Species richness	0.953	−0.048	0.005	38.70	5.94	8	36.90	4.53	8	20
32. Czeszczewik et al.	2014	Poland	Composition	Species richness	Bird communities	Species richness	0.976	−0.024	0.005	12.40	1.50	8	12.10	2.01	8	93
33. Sabatini et al.	2010	Italy	Composition	Species richness	Vascular plants	Species richness	1.030	0.029	0.013	27.10	7.38	10	27.90	6.65	10	200
34. Durak	2012	Poland	Composition	Species richness	Plant species (herb layer)	Species richness	1.062	0.060	0.006	26.44	8.98	32	28.07	7.07	30	28
35. Durak	2012	Poland	Composition	Species richness	Plant species (tree layer)	Species richness	1.065	0.063	0.018	2.16	1.39	32	2.30	0.92	30	28
36. Chumak et al.	2015	Ukraine	Composition	Species richness	Arthropods	Species richness	1.089	0.086	0.002	124.20	18.30	14	135.30	11.20	8	
37. Sitzia et al.	2012	Italy	Composition	Species richness	Understory vascular plants	Species richness	1.122	0.115	0.007	34.40	6.60	10	38.60	6.90	10	55
38. Boch et al.	2013	Germany	Composition	Species richness	Vascular plant species	Species richness	1.128	0.120	0.002	21.90	12.37	153	24.70	13.58	1152	20
39. Erdmann et al.	2006	Poland	Composition	Species richness	Oribatid mites	Species richness	1.167	0.154	0.042	9.00	2.80	4	10.50	2.80	4	160
40. Durak	2012	Poland	Composition	Species richness	Plant species (tree layer)	Species richness	1.170	0.157	0.010	1.94	0.72	32	2.27	0.91	30	77
41. Durak	2012	Poland	Composition	Species richness	Plant species (herb layer)	Species richness	1.187	0.172	0.005	22.91	4.59	32	27.20	8.65	30	77
42. Blaser et al.	2013	Germany	Composition	Species richness	Deadwood inhabiting fungi	Species richness	1.500	0.405	0.049	18.60	10.20	9	27.90	10.50	9	20
43. Durak	2012	Poland	Composition	Species richness	Plant species (shrub layer)	Species richness	1.503	0.407	0.011	1.91	0.89	32	2.87	1.07	30	28
44. Durak	2012	Poland	Composition	Species richness	Plant species (shrub layer)	Species richness	1.858	0.620	0.015	1.13	0.61	32	2.10	0.88	30	77

The references to the listed studies are listed in the supplementary material. The variables mean$^{\mathrm{unm}}$, and mean$^{\mathrm{man}}$, are the values of interest reported by the studies for unmanaged and managed stands, respectively. In the same way, SD$^{\mathrm{unm}}$, SD$^{\mathrm{man}}$, N^{unm}, and N^{man} are the corresponding standard deviations and sample sizes. ln$R$ is the effect size of the meta-analyses (equivalent to y_i in Eq. 4), the natural logarithm of mean$^{\mathrm{unm}}$/mean$^{\mathrm{man}}$, $v_{\ln R}$ is its variance, while R is the delogarithmized effect size mean$^{\mathrm{unm}}$/mean$^{\mathrm{man}}$. TSA (time since abandonment) is the time span in years since management had been abandoned in the unmanaged stands. 'Guild' refers to the taxa focused in the study

Table 2 Data used in the meta-analyses concerning stand structure

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean^{unm}	SD^{unm}	N^{unm}	Mean^{man}	SD^{man}	N^{man}	TSA
1. Boncina	2000	Slovenia	Stand structure	Maximum size	Number of trees per hectar with dbh >50 cm	0.253	−1.376	0.000	665.00	1.00	1	168.00	0.00	1	101
2. Boncina	2000	Slovenia	Stand structure	Stand density	Stem number (N ha^{-1})	1.483	0.394	0.000	265.00	1.00	1	393.00	0.00	1	101
3. Oheimb et al.	2004	Germany	Stand structure	Basal area	Basal area (m^2)	0.291	−1.236	0.092	26.50	7.40	18	7.70	5.10	5	45
4. Oheimb et al.	2004	Germany	Stand structure	Basal area	Basal area (m^2)	0.751	−0.286	0.025	18.10	8.40	21	13.60	4.30	7	45
5. Oheimb et al.	2004	Germany	Stand structure	Basal area	Basal area (m^2)	0.849	−0.163	0.001	38.50	7.50	70	32.70	3.10	14	45
6. Oheimb et al.	2004	Germany	Stand structure	Basal area	Basal area (m^2)	0.914	−0.089	0.004	26.90	6.10	23	24.60	4.90	31	45
7. Oheimb et al.	2004	Germany	Stand structure	Basal area	Basal area (m^2)	1.311	0.271	0.008	22.50	6.00	18	29.50	3.60	4	45
8. Oheimb et al.	2004	Germany	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.034	−3.385	0.046	209.50	109.50	18	7.10	2.50	4	45
9. Oheimb et al.	2004	Germany	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.046	−3.072	0.096	284.80	86.00	21	13.20	10.60	7	45
10. Oheimb et al.	2004	Germany	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.065	−2.736	0.051	163.50	82.00	23	10.60	11.80	31	45
11. Oheimb et al.	2004	Germany	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.128	−2.055	0.120	200.70	81.70	18	25.70	19.10	5	45
12. Oheimb et al.	2004	Germany	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.158	−1.847	0.053	61.50	45.60	70	9.70	7.70	14	45
13. Oheimb et al.	2004	Germany	Stand structure	Diversity	Mean diameter differentiation	0.693	−0.367	0.067	0.40	0.12	18	0.28	0.16	5	45
14. Oheimb et al.	2004	Germany	Stand structure	Diversity	Mean diameter differentiation	0.714	−0.337	0.019	0.36	0.09	21	0.26	0.09	7	45
15. Oheimb et al.	2004	Germany	Stand structure	Diversity	Mean diameter differentiation	0.808	−0.213	0.005	0.31	0.07	70	0.25	0.06	14	45
16. Oheimb et al.	2004	Germany	Stand structure	Diversity	Mean diameter differentiation	0.839	−0.175	0.011	0.32	0.12	23	0.27	0.10	31	45
17. Laiolo et al.	2004	Italy	Stand structure	Diversity	Variability in dbh	0.861	−0.150	0.008	37.30	19.60	166	32.10	19.00	59	40
18. Laiolo et al.	2004	Italy	Stand structure	Diversity	Variability in stand density	0.888	−0.119	0.007	60.70	34.60	166	53.90	29.60	59	40
19. Oheimb et al.	2004	Germany	Stand structure	Diversity	Mean diameter differentiation	1.014	0.014	0.003	0.29	0.06	18	0.29	0.02	4	45

Table 2 continued

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
20. Laiolo et al.	2004	Italy	Stand structure	Mean diameter	Mean diameter (cm)	0.850	−0.162	0.002	29.40	10.00	166	25.00	6.90	59	40
21. Laiolo et al.	2004	Italy	Stand structure	Stand density	Tree density	1.000	0.000	0.006	0.40	0.20	166	0.40	0.20	59	40
22. Commarmot et al.	2005	Ukraine/ Switzerland	Stand structure	Basal area	Basal area (m^2)	1.254	0.226	0.002	30.70	5.30	40	38.50	7.40	40	45
23. Commarmot et al.	2005	Ukraine/ Switzerland	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.072	−2.630	0.068	111.00	61.40	40	8.00	12.40	40	45
24. Christensen et al.	2005	Europe	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.187	−1.676	0.069	625.00	110.00	16	117.00	74.00	6	50
25. Christensen et al.	2005	Europe	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.750	−0.288	0.037	132.00	70.00	20	99.00	98.00	43	50
26. Commarmot et al.	2005	Ukraine/ Switzerland	Stand structure	Mean diameter	Mean diameter (cm)	0.867	−0.143	0.002	48.00	6.90	40	41.60	8.30	40	45
27. Commarmot et al.	2005	Ukraine/ Switzerland	Stand structure	Stand density	Stem number (N ha^{-1})	0.846	−0.168	0.009	259.00	143.50	40	219.00	46.90	40	45
28. Chumak et al.	2005	Switzerland	Stand structure	Stand density	Number of individuals (total)	1.877	0.630	0.027	2530.25	637.43	4	4750.00	1019.88	4	65
29. Friedel et al.	2006	Germany	Stand structure	Basal area	Basal area (m^2)	1.000	0.000	0.005	25.00	9.00	45	25.00	8.00	45	50
30. Debeljak	2006	Slovenia	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.155	−1.864	0.060	378.43	168.85	4	58.65	11.65	4	–
31. Friedel et al.	2006	Germany	Stand structure	Mean diameter	Mean diameter (cm)	0.902	−0.103	0.005	51.00	28.00	100	46.00	22.00	100	50
32. Friedel et al.	2006	Germany	Stand structure	Microhabitats	Number of growth of anomalies per tree	0.556	−0.588	2.572	0.90	1.00	100	0.50	8.00	100	50
33. Friedel et al.	2006	Germany	Stand structure	Stand density	Stem number (N ha^{-1})	1.444	0.368	0.088	270.00	260.00	45	390.00	680.00	45	50
34. Merino et al.	2007	Spain	stand structure	basal area	basal area (m^2)	0.783	−0.244	0.009	48.00	19.40	32	37.60	10.70	21	101
35. Müller et al.	2007	Germany	stand structure	deadwood	deadwood volume (m^3 ha^{-1})	0.180	−1.717	0.107	172.67	88.32	3	31.00	10.60	6	25
36. Merino et al.	2007	Spain	Stand structure	Diversity	Gini coefficient (variation in dbh)	0.889	−0.118	0.006	0.27	0.09	32	0.24	0.06	21	101
37. Müller et al.	2007	Germany	Stand structure	Mean diameter	Mean diameter (cm)	0.673	−0.395	0.002	74.00	3.46	3	49.83	3.76	6	25
38. Merino et al.	2007	Spain	Stand structure	Mean diameter	Mean diameter (cm)	0.769	−0.262	0.004	29.90	7.90	32	23.00	4.50	21	101

Table 2 continued

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
39. Müller et al.	2007	Germany	Stand structure	Stand density	Canopy cover (%)	0.979	−0.022	0.027	70.33	13.58	3	68.83	20.03	6	25
40. Merino et al.	2007	Spain	Stand structure	Stand density	Stem number (N ha^{-1})	1.333	0.287	0.009	568.90	238.40	32	758.30	213.40	21	101
41. Burrascano et al.	2008	Italy	Stand structure	Basal area	Basal area (m^2)	1.280	0.247	0.006	30.70	6.30	16	39.30	9.30	16	101
42. Winter and Möller	2008	Germany	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.061	−2.798	0.031	231.50	17.68	2	14.10	7.43	10	101
43. Burrascano et al.	2008	Italy	Stand structure	Deadwood	Total amount of deadwood (m^3 ha^{-1})	0.269	−1.313	0.067	45.00	39.90	16	12.10	6.50	16	101
44. Burrascano et al.	2008	Italy	Stand structure	Diversity	Number of diameter classes	0.777	−0.253	0.004	9.40	1.80	16	7.30	1.30	16	101
45. Burrascano et al.	2008	Italy	Stand structure	Maximum size	Number of trees per hectare with dbh >40 cm	0.243	−1.414	0.071	7.40	2.80	16	1.80	1.80	16	101
46. Winter and Möller	2008	Germany	Stand structure	Microhabitats	Number of habitat structures per hectare	0.328	−1.115	0.023	251.44	197.51	37	82.47	83.86	161	101
47. Burrascano et al.	2008	Italy	Stand structure	Stand density	Tree cover	1.382	0.324	0.003	66.70	15.40	16	92.20	2.60	16	101
48. Winter and Möller	2008	Germany	Stand structure	Stand density	Stem number (N ha^{-1})	2.529	0.928	0.253	837.50	123.74	2	2118.30	3297.42	10	101
49. Bütler and Lachat	2009	Switzerland	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.140	−1.965	0.019	119.20	108.76	96	16.70	16.66	96	30
50. Bütler and Lachat	2009	Switzerland	Stand structure	Maximum size	Number of trees per hectare with dbh >60 cm	0.630	−0.461	0.015	4.60	2.88	92	2.90	2.88	92	30
51. Bütler and Lachat	2009	Switzerland	Stand structure	Microhabitats	Number of habitat structures per hectare	0.453	−0.791	0.042	430.00	338.03	24	195.00	122.47	24	30
52. Bütler and Lachat	2009	Switzerland	Stand structure	Microhabitats	Number of habitat structures per hectare	0.400	−0.917	0.022	498.00	186.16	24	199.00	122.47	24	30
53. Bütler and Lachat	2009	Switzerland	Stand structure	Microhabitats	Number of habitat structures per hectare	0.505	−0.682	0.030	279.00	161.67	24	141.00	88.18	24	30
54. Bütler and Lachat	2009	Switzerland	Stand structure	Microhabitats	Number of habitat structures per hectare	0.498	−0.698	0.024	207.00	93.08	24	103.00	63.69	24	30

Table 2 continued

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\text{unm}}$	SD$^{\text{unm}}$	N^{unm}	Mean$^{\text{man}}$	SD$^{\text{man}}$	N^{man}	TSA
55. Paillet and Satre	2010	France	Stand structure	Basal area	Basal area (m^2)	0.946	−0.055	0.014	40.90	4.92	5	38.70	9.17	5	10
56. Paillet and Satre	2010	France	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.235	−1.448	0.538	85.50	84.08	5	20.10	26.39	5	10
57. Vuidot et al.	2011	France	Stand structure	Basal area	Basal area (m^2)	1.090	0.086	0.016	16.70	6.60	11	18.20	2.90	12	40
58. Bilek et al.	2011	Czech Republic	Stand structure	Basal area	Basal area (m^2)	0.967	−0.034	0.011	33.20	3.39	4	32.10	6.02	4	55
59. Vuidot et al.	2011	France	Stand structure	Basal area	Basal area (m^2)	0.873	−0.135	0.010	24.50	6.20	12	21.40	5.20	13	151
60. Vuidot et al.	2011	France	Stand structure	Basal area	Basal area (m^2)	0.727	−0.318	0.014	36.30	5.50	5	26.40	5.80	5	30
61. Vuidot et al.	2011	France	Stand structure	Basal area	Basal area (m^2)	0.946	−0.055	0.014	40.90	5.00	5	38.70	9.20	5	10
62. Vuidot et al.	2011	France	Stand structure	Basal area	Basal area (m^2)	0.715	−0.336	0.033	29.80	7.30	3	21.30	4.90	4	20
63. Bilek et al.	2011	Czech Republic	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.054	−2.911	0.092	40.90	10.18	2	2.23	1.10	4	55
64. Vuidot et al.	2011	France	Stand structure	Deadwood	Mean deadwood volume (m^3 ha^{-1})	0.105	−2.255	0.072	175.40	85.80	12	18.40	15.20	13	151
65. Vuidot et al.	2011	France	Stand structure	Deadwood	Mean deadwood volume (m^3 ha^{-1})	0.235	−1.448	0.536	85.50	84.10	5	20.10	26.30	5	10
66. Vuidot et al.	2011	France	Stand structure	Deadwood	Mean deadwood volume (m^3 ha^{-1})	0.431	−0.841	0.192	44.50	54.00	11	19.20	16.10	12	40
67. Vuidot et al.	2011	France	Stand structure	Deadwood	Mean deadwood volume (m^3 ha^{-1})	1.292	0.256	0.130	31.90	18.30	5	41.20	23.40	5	30
68. Vuidot et al.	2011	France	Stand structure	Deadwood	Mean deadwood volume (m^3 ha^{-1})	1.498	0.404	0.282	31.70	21.90	3	47.50	33.30	4	20
69. Bilek et al.	2011	Czech Republic	Stand structure	Diversity	Variation in dbh (SD)	0.419	−0.870	0.021	29.36	7.88	4	12.30	1.27	4	55
70. Bilek et al.	2011	Czech Republic	Stand structure	Maximum size	Maximum diameter (cm)	0.861	−0.150	0.002	109.20	1.41	4	93.98	7.87	4	55
71. Bilek et al.	2011	Czech Republic	Stand structure	Mean diameter	Mean diameter (cm)	1.433	0.360	0.012	42.35	9.12	4	60.70	3.22	4	55
72. Vuidot et al.	2011	France	Stand structure	Microhabitats	Number of microhabitats per tree	1.066	0.063	0.005	2.04	0.63	36	2.18	0.72	39	50
73. Bilek et al.	2011	Czech Republic	Stand structure	Stand density	Stem number (N ha^{-1})	0.465	−0.765	0.014	237.50	48.79	4	110.50	13.58	4	55

Table 2 continued

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
74. Sitzia et al.	2012	Italy	Stand structure	Basal area	Basal area (m^2)	1.079	0.076	0.011	46.80	10.00	10	50.50	13.20	10	55
75. Visnic et al.	2012	Bosnia	Stand structure	Basal area	Basal area (m^2)	0.839	−0.176	0.003	45.28	8.69	35	37.99	5.96	17	40
76. Larrieu et al.	2012	France	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.342	−1.072	0.006	49.48	10.77	19	16.94	4.49	21	50
77. Sitzia et al.	2012	Italy	Stand structure	Deadwood	Coarse wood debris (m^3 ha^{-1})	0.642	−0.442	0.019	38.60	9.90	10	24.80	8.80	10	55
78. Sitzia et al.	2012	Italy	Stand structure	Diversity	Tree diameter variation	1.053	0.051	0.002	1.90	0.20	10	2.00	0.20	10	55
79. Paffeti et al.	2012	Italy	Stand structure	Mean diameter	Mean diameter (cm)	0.438	−0.825	0.002	63.35	36.50	184	27.75	8.50	496	400
80. Visnic et al.	2012	Bosnia	Stand structure	Stand density	Stem number (N ha^{-1})	2.333	0.847	0.021	429.00	337.19	35	1001.00	228.23	17	40
81. Toïgo et al.	2013	France	Stand structure	Basal area	Basal area (m^2)	0.900	−0.105	0.007	25.00	11.70	42	22.50	6.80	43	30
82. Blaser et al.	2013	Germany	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.554	−0.590	0.033	17.50	5.54	9	9.70	4.33	9	20
83. Toïgo et al.	2013	France	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.609	−0.495	0.055	34.30	33.50	42	20.90	24.60	43	30
84. Nascimbene et al.	2013	Italy	Stand structure	Stand density	Canopy cover (%)	0.897	−0.108	0.001	88.60	5.70	10	79.50	6.80	10	60
85. Larrieu et al.	2014	France	Stand structure	Basal area	Basal area (m^2)	0.919	−0.084	0.009	39.70	11.71	17	36.5	10.08	21	110
86. Larrieu et al.	2014	France	Stand structure	Mean diameter	Mean diameter (cm)	0.678	−0.389	0.147	59.00	72.80	17	40	43.80	21	110
87. Czeszczewik et al.	2015	Poland	Stand structure	Deadwood	Basal area of snags (m^2)	0.054	−2.927	0.041	11.02	1.21	8	0.59	0.33	8	–
88. Czeszczewik et al.	2015	Poland	Stand structure	Deadwood	Basal area of snags (m^2)	0.237	−1.438	0.026	3.79	1.35	8	0.9	0.25	8	–
89. Czeszczewik et al.	2015	Poland	Stand structure	Deadwood	Basal area of snags (m^2)	0.349	−1.053	0.007	5.25	0.61	8	1.832	0.37	8	–
90. Motta et al.	2015	Italy. Bosnia. Montenegro	Stand structure	Basal area	Basal area (m^2)	0.689	−0.373	0.002	60.40	3.89	102	41.6	3.51	48	–
91. Motta et al.	2015	Italy. Bosnia. Montenegro	Stand structure	Diversity	Diameter diversity	0.664	−0.410	0.001	24.70	2.58	102	16.4	2.35	48	–
92. Motta et al.	2015	Italy. Bosnia. Montenegro	Stand structure	Maximum_size	Number of trees per hectare with dbh >50 cm	0.696	−0.363	0.002	92.00	11.10	102	64	17.90	48	–

Table 2 continued

Study	Year	Country	Biodiversity component	Subcategory	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{unm}}$	SD$^{\mathrm{unm}}$	N^{unm}	Mean$^{\mathrm{man}}$	SD$^{\mathrm{man}}$	N^{man}	TSA
93. Motta et al.	2015	Italy. Bosnia. Montenegro	Stand structure	Mean diameter	Mean diameter (cm)	0.811	−0.209	0.001	39.70	3.76	102	32.2	6.83	48	–
94. Pach and Podlaski	2015	Polen	Stand structure	Basal area	Basal area (m^2)	1.221	0.200	0.005	35.38	12.73	30	43.21	5.06	32	–
95. Pach and Podlaski	2015	Polen	Stand structure	Diversity	Diameter diversity	0.562	−0.575	0.002	14.40	1.64	30	8.1	1.99	32	–
96. Pach and Podlaski	2015	Polen	Stand structure	Maximum size	Maximum diameter (cm)	0.564	−0.573	0.003	80.30	15.10	30	45.3	9.40	32	–
97. Paillet et al.	2015	France	Stand structure	Maximum size	Basal area large diameter trees per hectare (>67.5 cm)	0.937	−0.066	0.0120	6.30	5.74	115	5.9	4.43	118	46
98. Paillet et al.	2015	France	Stand structure	Stand density	Stem number (N ha^{-1})	0.810	−0.211	0.007	618.10	370.96	115	500.5	340.02	118	46
99. Paillet et al.	2015	France	Stand structure	Deadwood	Deadwood volume (m^3 ha^{-1})	0.231	−1.464	0.056	52.3	44.86	115	12.1	29.37	118	46
100. Paillet et al.	2015	France	Stand structure	Basal area	Basal area (m^2)	0.854	−0.158	0.001	28.00	7.66	115	23.9	6.93	118	46

The references to the listed studies are listed in the supplementary material. The variables mean$^{\mathrm{unm}}$, and mean$^{\mathrm{man}}$, are the values of interest reported by the studies for unmanaged and managed stands, respectively. In the same way, SD$^{\mathrm{unm}}$, SD$^{\mathrm{man}}$, N^{unm}, and N^{man} are the corresponding standard deviations and sample sizes. ln$R$ is the effect size of the meta-analyses (equivalent to y_i in Eq. 4), the natural logarithm of mean$^{\mathrm{unm}}$/mean$^{\mathrm{man}}$, $v_{\ln R}$ is its variance, while R is the delogarithmized effect size mean$^{\mathrm{unm}}$/mean$^{\mathrm{man}}$. TSA (time since abandonment) is the time span in years since management had been abandoned in the unmanaged stands species density to more complex indicators like the Shannon index (Shannon and Weaver 1949) or Simpson index (Simpson 1949). Terminology was not always used consistently by authors (cf. critique of quantifying species richness by Gotelli and Colwell 2001, similarly Spellerberg and Fedor 2003), excluding a considerable number of potentially interesting studies from our meta-analysis. We concentrated on response variables belonging to the subcategories (1) species richness and (2) species diversity, which were the most frequently reported in the literature. Species richness in our context simply means the numbers of species sampled in a given forest stand, while indicators relating species diversity also take into account species abundancy and the Shannon index. For both, species richness and diversity, we did not differentiate by taxonomic groups in the meta-analysis due to the limited number of eligible studies.

When assembling study results for the meta-analysis, we had to take care for not to introduce a lack of statistical independence (Viechtbauer 2010). Since several papers reported more than one equivalent response variable per subcategory, for instance Sitzia et al. (2012) analysed height and diameter diversity of the same experiment, we only used the one with the highest sample size. If one study reported different levels of a response variable (e.g. species richness of bryophytes together with species richness of all plants, or amount of snag deadwood together with total deadwood amount), we always took the most aggregating level into account (in the example: species richness of all plants and total deadwood amount). If one study reported analogous results from very different objects (e.g. stands, forest areas) which were obviously independent in a statistical sense, we treated each of them like a separate study in the meta-analysis. In doubt, however, we calculated in such a case the sample-size-weighted mean of the response variable across all objects together with its standard deviation. We dealt this way, for example, with the results shown by Müller et al. (2007) who present comparisons between different but similar thinning experiments and unmanaged stands.

The biodiversity component “function” was addressed by stand productivity regulated mainly by thinning and species composition and mixing regulation. The potential of continuous moderate thinning to increase stand productivity by up to 20% is well corroborated by numerous studies since the beginning of systematic forest science (e.g. Assmann 1970; Pretzsch 2005b; Pretzsch et al. 2017; Schwappach 1893; Wiedemann 1951). Establishment and management of mixed species stands—as an a priori decision for higher functional diversity (see “Introduction” section)—is a second, but less well analysed silvicultural measure for promoting stand productivity and functioning. Without human influence, many Central European forest stands would at least temporarily consist of more than one tree species. So, tree species mixture is of special interest in the context of this study, as it can be seen as a management option and a diversity aspect at the same time. Data were taken from Pretzsch et al. (2013a, b) and Pretzsch et al. (2010) (Table 3) who present extensive results from long-term growth and yield plots where mixed stand growth (in terms of merchantable wood production, m^3 ha^{-1} a^{-1}) is related to the growth of pure stands. In total, the above-mentioned studies report 53 such comparisons covering the species combinations Norway spruce (*Picea abies* (L.) KARST.)—European beech (*F. sylvatica* L.), European Oak (*Quercus* sp. = *Q. robur* L. and *Q. petraea* (MATT.) LIEBL.)—European beech, and Norway spruce—Silver fir (*Abies alba* MILL.)—European beech. As each such comparison was completely independent from all others in a statistical sense, we treated each like a separate study in the meta-analysis.

As response variable we compared the merchantable wood volume increment (m^3 ha^{-1} a^{-1}) of mixed and pure stands. The former is given as the observed productivity of the mixed stand $p_{1,2}$ (consisting of species 1 and 2). The latter is given by the productivity expected for the mixed stand, $\hat{p}_{1,2}$, under the assumption that mixture has no influence on productivity, i.e. that mixed and pure stands are not different in terms of productivity (cf. Pretzsch et al. 2013a, p. 268). In detail, this expected productivity $\hat{p}_{1,2}$ was derived from the productivity of both species in the neighbouring pure stands, p_1 and p_2, and their mixing portions m_1 and m_2 in the mixed stand ($\hat{p}_{1,2} = m_1 \times p_1 + m_2 \times p_2$). In each comparison mixed and pure stands are comparable in terms of site conditions and stand age in order to minimize such confounding influences.

Definition of stand management practices

Not all of the studies we considered in our meta-analyses did give a clear definition of what practices they considered to be management. However, harvest operations, or more specifically thinnings, were mentioned most often as typical management manifestations. Thinning, in contrast to final felling, is the selective removal of trees from a premature forest stand without the purpose of demounting the stand and thereby creating space for the next forest generation. In general, the purpose of thinnings can be to steer the remaining stand’s development, and/or to gain economic profit extracting commercial wood from premature stands. It is widely accepted to define a thinning by the three parameters kind of thinning, severity, and intensity (Assmann 1970; Abetz and Mitscherlich 1969). The kind of thinning comprises the concept which is behind

Table 3 Data used in the meta-analyses concerning productivity of mixed versus pure stands

Trial*	Country	Species combination	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\text{mixture}}$	SD$^{\text{mixture}}$	N^{mixture}	Mean$^{\text{pure}}$	SD$^{\text{pure}}$	N^{pure}
1. Ehingen 51	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	0.870	−0.139	0.010	0.87	0.12	2	1.00	0.00	2
2. Wiedemann 1951	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	0.951	−0.051	0.003	0.95	0.16	9	1.00	0.00	9
3. Mitterteich 101	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	0.978	−0.022	0.001	0.98	0.06	8	1.00	0.00	8
4. Westerhof 131b37	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	0.990	−0.010	0.002	0.99	0.16	15	1.00	0.00	15
5. Westerhof 131b31	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	0.991	−0.009	0.011	0.99	0.27	7	1.00	0.00	7
6. Wieda 114	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.051	0.050	0.001	1.05	0.08	9	1.00	0.00	9
7. Zwiesel 111	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.071	0.068	0.002	1.07	0.20	20	1.00	0.00	20
8. Uslar 57	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.106	0.101	0.007	1.11	0.44	22	1.00	0.00	22
9. Daun 1207	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.135	0.126	0.009	1.13	0.31	8	1.00	0.00	8
10. Zwiesel 134	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.135	0.127	0.008	1.14	0.21	4	1.00	0.00	4
11. Knobben 44 1/2	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.138	0.129	0.002	1.14	0.14	9	1.00	0.00	9
12. Oderhaus 602	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.151	0.141	0.003	1.15	0.25	16	1.00	0.00	16
13. Daun 1206	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.180	0.165	0.004	1.18	0.22	8	1.00	0.00	8
14. Zwiesel 135	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.195	0.178	0.001	1.19	0.09	8	1.00	0.00	8
15. Geislingen 76	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.252	0.225	0.013	1.25	0.49	12	1.00	0.00	12
16. Morbach 1501	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.300	0.262	0.020	1.30	0.52	8	1.00	0.00	8
17. Freising 813	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.592	0.465	0.011	1.59	0.47	8	1.00	0.00	8
18. Nordhalben 811	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.704	0.533	0.004	1.70	0.25	5	1.00	0.00	5
19. Murten 20	Switzerland	Norway spruce–European beech	Relative productivity between mixed and pure stands	1.999	0.693	0.008	2.00	0.50	8	1.00	0.00	8
20. Schongau 814	Germany	Norway spruce–European beech	Relative productivity between mixed and pure stands	2.025	0.705	0.022	2.02	1.01	11	1.00	0.00	11

Table 3 continued

Trial*	Country	Species combination	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\mathrm{mixture}}$	SD$^{\mathrm{mixture}}$	N^{mixture}	Mean$^{\mathrm{pure}}$	SD$^{\mathrm{pure}}$	N^{pure}
21. Concise	Switzerland	Oak**–European beech	Relative productivity between mixed and pure stands	0.732	−0.312	0.010	0.73	0.41	33	1.00	0.00	33
22. Waldbrunn 106	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	0.842	−0.172	0.000	0.84	0.05	10	1.00	0.00	10
23. Gryfino 35	Poland	Oak**–European beech	Relative productivity between mixed and pure stands	0.857	−0.154	0.002	0.86	0.10	7	1.00	0.00	7
24. Dhronecken	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	0.946	−0.056	0.007	0.95	0.28	13	1.00	0.00	13
25. Gryfino 33	Poland	Oak**–European beech	Relative productivity between mixed and pure stands	0.962	−0.039	0.003	0.96	0.20	14	1.00	0.00	14
26. Ebrach 132	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	0.969	−0.031	0.017	0.97	0.18	2	1.00	0.00	2
27. Waldbrunn 105	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.005	0.005	0.003	1.00	0.17	10	1.00	0.00	10
28. Main-Tauber 86	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.039	0.039	0.001	1.04	0.07	7	1.00	0.00	7
29. Jossgrund 151	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.117	0.111	0.002	1.12	0.29	32	1.00	0.00	32
30. Ebrach 133	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.233	0.210	0.016	1.23	0.35	5	1.00	0.00	5
31. Hochstift 619	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.238	0.213	0.005	1.24	0.30	11	1.00	0.00	11
32. Schluechtern 56	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.270	0.239	0.022	1.27	0.62	11	1.00	0.00	11
33. Hochstift 618	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.299	0.262	0.002	1.30	0.19	10	1.00	0.00	10
34. Balmis	Switzerland	Oak**–European beech	Relative productivity between mixed and pure stands	1.416	0.348	0.001	1.42	0.18	14	1.00	0.00	14
35. Hochstift 617	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	1.483	0.394	0.002	1.48	0.25	12	1.00	0.00	12
36. Eichbuehl	Switzerland	Oak**–European beech	Relative productivity between mixed and pure stands	1.800	0.588	0.027	1.80	0.73	6	1.00	0.00	6
37. Rothenbuch 801	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	2.242	0.807	0.008	2.24	0.66	11	1.00	0.00	11
38. Kelheim 804	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	2.428	0.887	0.012	2.43	0.53	4	1.00	0.00	4
39. Rohrbrunn 314	Germany	Oak**–European beech	Relative productivity between mixed and pure stands	2.532	0.929	0.021	2.53	0.74	4	1.00	0.00	4

Table 3 continued

Trial*	Country	Species combination	Measure (unit)	R	ln$R$	$v_{\ln R}$	Mean$^{\text{mixture}}$	SD$^{\text{mixture}}$	N^{mixture}	Mean$^{\text{pure}}$	SD$^{\text{pure}}$	N^{pure}
40. Kreuth 120	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	0.708	−0.346	0.003	0.71	0.11	8	1.00	0.00	8
41. Partenkirchen 115	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	0.748	−0.291	0.040	0.75	0.21	2	1.00	0.00	2
42. Kreuth 125	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	0.847	−0.166	0.006	0.85	0.15	6	1.00	0.00	6
43. Ruhpolding 113	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	0.986	−0.014	0.000	0.99	0.04	4	1.00	0.00	4
44. Kreuth 123	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.008	0.008	0.018	1.01	0.31	5	1.00	0.00	5
45. Ruhpolding 116	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.208	0.189	0.073	1.21	0.46	2	1.00	0.00	2
46. Kreuth 126	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.222	0.201	0.012	1.22	0.19	2	1.00	0.00	2
47. Kreuth 124	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.336	0.290	0.000	1.34	0.03	2	1.00	0.00	2
48. Freyung 129	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.483	0.394	0.003	1.48	0.26	12	1.00	0.00	12
49. Bodenmais 130	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.484	0.395	0.002	1.48	0.12	4	1.00	0.00	4
50. Kreuth 122	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.489	0.398	0.014	1.49	0.51	8	1.00	0.00	8
51. Kreuth 824	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.493	0.401	0.029	1.49	0.36	2	1.00	0.00	2
52. Traunstein 147	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.585	0.460	0.002	1.58	0.17	6	1.00	0.00	6
53. Marquartstein 108	Germany	Silver fir–Norway spruce–European beech	Relative productivity between mixed and pure stands	1.687	0.523	0.004	1.69	0.18	3	1.00	0.00	3

The listed trials are described in Pretzsch et al. (2010), and Pretzsch et al. (2013a, b). The variables R, ln$R$, $v_{\ln R}$, mean, SD, N have the same meaning as explained with Tables 1 and 2, just for mixed and pure stands instead of unmanaged and managed ones. As for each trial directly the ratio of the productivity mixed/pure was reported, the mean value and standard deviation of the pure stands reduce to 1 and 0, respectively

* Data originated from Pretzsch et al. (2010) and Pretzsch et al. (2013a, b)

** *Quercus* sp. = *Q. robur* L. and *Q. petraea* (MATT.) LIEBL selecting the removal trees like thinning from below, thinning from above, or selective thinning. Thinning severity addresses the amount of wood volume which is removed during one thinning activity. Finally, the thinning intensity characterizes the time interval between two thinning activities, e.g. short (like, e.g. 3 years) or rather long (e.g. 15–20 years).

The thinning or harvest types reported in the studies covering structural diversity and species composition comprised methods like selective thinning, thinning from below, shelterwood concepts, group selection logging, or selection forest systems. However, the amount of usable study results was too small to test the influence of such different silvicultural practices. In addition, the available treatment definitions often did not allow unambiguous distinctions. Thus, we had to stick to the coarse distinction between managed and unmanaged forest and, however, partly with the possibility to take into account how long ago management had been abandoned.

Our data concerning the biodiversity component "function"—represented by aboveground biomass productivity—do not contain any differentiation between managed and unmanaged forest stands. Here, we compare and interpret the cultivation of mixed species stands as opposed to monospecific stands as two different silvicultural options which require different ways of stand establishment as well as different thinning concepts, e.g. for reducing interspecific competition in mixed stands.

Statistical analyses

If several studies $i = 1, \ldots, k$ are to be combined in a meta-analysis, the effect y_i observed in the ith study can be seen as the sum of the unknown true effect θ_i and the sampling error e_i which is assumed to be normally distributed with a mean of zero and the sampling variance v_i ($e_i \sim N(0, v_i)$, cf. Viechtbauer 2010):

$$y_i = \theta_i + e_i \tag{1}$$

The goal of the meta-analysis is to estimate the average true effect. As the studies probably differ in terms of methods, sample characteristics, etc., heterogeneity among the true effects has to be taken into account

$$\theta_i = \mu + u_i \tag{2}$$

The average true effect in Eq. 2 is μ, and u_i is a study-specific random effect taking into account the above-mentioned heterogeneity ($u_i \sim N(0, \tau^2)$).

Equation 2 was the basic model we applied in order to test for a significant management effect (managed vs. unmanaged) on species diversity and selected aspects of structural diversity. We also used it for testing the effect of species mixture (mixed vs. pure) on productivity. If, when testing the effect of managed versus unmanaged, the time since management abandonment, TSA, was reported in a part of the studies, we conducted a second analysis based on those studies including TSA as a moderator variable:

$$\theta_i = \beta_0 + \beta_1 \cdot TSA_i + u_i \tag{3}$$

A significant deviation of β_1 from 0 indicates a significant influence of TSA on the average true effect. As Viechtbauer (2010) states, u_i represents the residual heterogeneity among the true effects, in this case.

As the effect size for all analyses in this study, we used the log-transformed ratio of means (Hedges et al. 1999). Assume, study i reports a mean outcome m_{r} for the reference category (unmanaged or pure stands) and a mean outcome m_{t} for the treatment category (managed or mixed stands), then the study's effect y_i (cf. Eq. 1) results as:

$$y_i = \ln\left(\frac{m_{\mathrm{t}}}{m_{\mathrm{r}}}\right) \tag{4}$$

Thus, our meta-analyses test for significant relative deviations of (1) diversity measures of managed related to unmanaged forests, and (2) productivity of mixed related to pure stands. We conducted the analysis with the free software package R (R Core Team 2015), namely the package metafor (Viechtbauer 2010).

Results

Response of species richness and species diversity to forest stand management

As indicated by the pairwise comparisons of the entire data set (Fig. 2), the single study outcomes were very heterogeneous; species richness (without any differentiation by taxonomic groups, $n = 29$ comparisons) and diversity ($n = 15$ comparisons) were decreased, balanced, or increased in managed compared with unmanaged stands. In total, for the delogarithmized effect size R ($R = e^y$, with y being the effect size of Eq. 4), a range of $R = 0.43$–1.86 (richness) and 0.13–3.39 (diversity), respectively, was given. On average, the overall estimate for R was 0.96 for species richness and 1.0 for species diversity with no significant deviation from 1.0 ($p > 0.05$, see Fig. 2). Thus, we could not detect any clear relationship of compositional diversity with forest stand management.

Based on the studies which reported time since abandonment of management (species richness: $n = 28$; species diversity: $n = 14$), the global effect of time since abandonment of management was significant neither for species richness nor for species diversity ($p > 0.05$, Table 4).

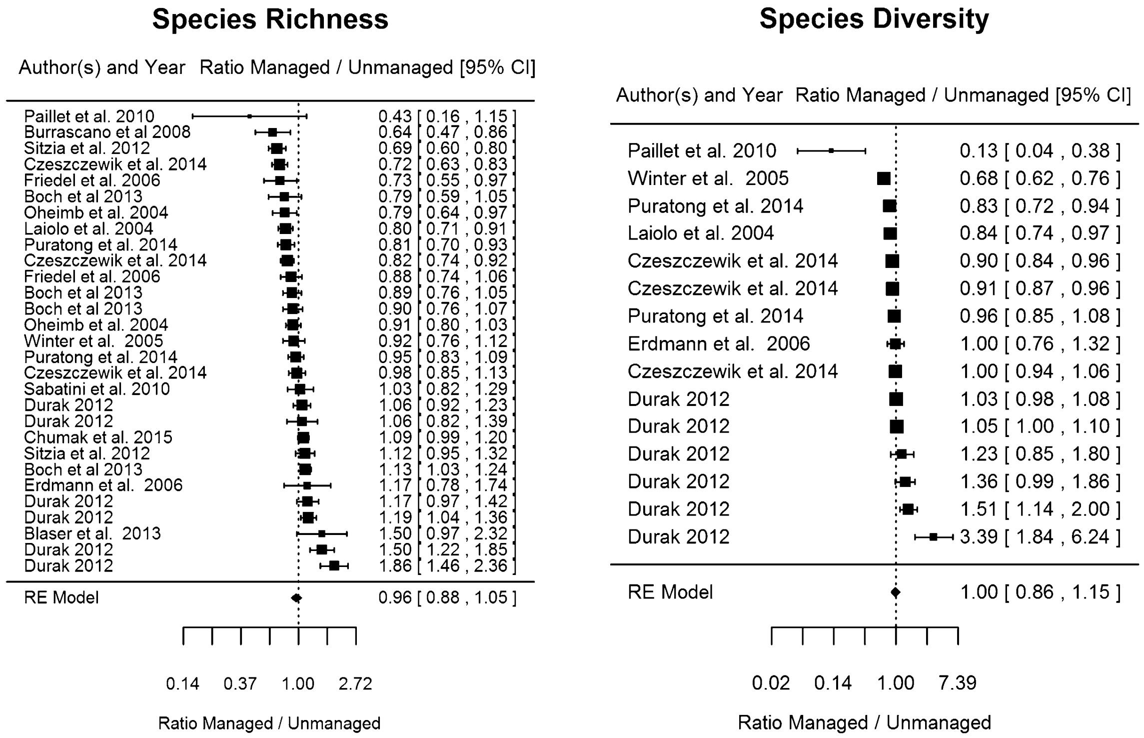

Fig. 2 Meta-analysis outcomes for species richness (*left*) and species diversity (*right*). Ratio managed/unmanaged is the delogarithmized effect size of Eq. 4. The *bottom line* shows the estimated overall effect size and its 95% confidence interval (CI) as a rhomb. If this shape does not touch the *dashed 1.0-line*, this indicates a significant ($p < 0.05$) management effect. The *lines above* show the single comparison-wise results together with their CI

Table 4 Meta-analysis outcomes for species richness and species diversity including time since abandonment of management (TSA) according to Eq. 3

Category	N	Intercept β_0 (±SE)	Slope β_1 (±SE)
Species richness	28	-0.062 ± 0.078	$0.000 \pm 0.001^{\text{n.s.}}$
Species diversity	14	-0.197 ± 0.204	$0.004 \pm 0.003^{\text{n.s.}}$

The slope β_1 is, in both cases nonsignificantly different from zero (n.s.)

Response of structural features to forest stand management

While the single studies differ considerably in their outcomes (Fig. 3), five out of seven investigated stand structure features respond significantly to management (Table 5). We obtained the strongest effect for deadwood with the estimated delogarithmized effect size R (=ratio managed/unmanaged) amounting to 0.19 only ($p < 0.0001$). Strong effects were also found for the number of microhabitats ($R = 0.51$, $p < 0.0001$) and maximum tree size indicators ($R = 0.54$, $p < 0.003$). For size diversity, the estimate of R is 0.77 ($p < 0.0001$) and 0.79 for mean tree size ($p = 0.03$). Stand basal area and number of living trees per unit area do not show any significant effect. In other words, especially structural features which are often considered to be positively linked to biodiversity, like tree size, its diversity, the number of microhabitats, and deadwood amount are considerably lower in managed forests. This is not the case for traditional measures of stand density as basal area and number of living trees.

Not all of the studies taken into account reported time since abandonment of management (TSA). Thus, only a subset of the available studies on structural features could be used in this context. The meta-analyses according to Eq. 3 yielded significant results ($p \leq 0.01$) for the global TSA effect in the case of mean tree size and maximum size (Table 6). Time since abandonment of management activities had a negative effect on both covariates. Thus, the more time elapsed after management had been abandoned in unmanaged stands, the smaller they are in managed forests relative to unmanaged ones.

Tree species mixing and productivity

The following meta-analytical review of the primary effect of mixing on productivity is based on an analysis of long-term experimental plots along ecological gradients in Central Europe (Pretzsch et al. 2010, 2013a, b). As

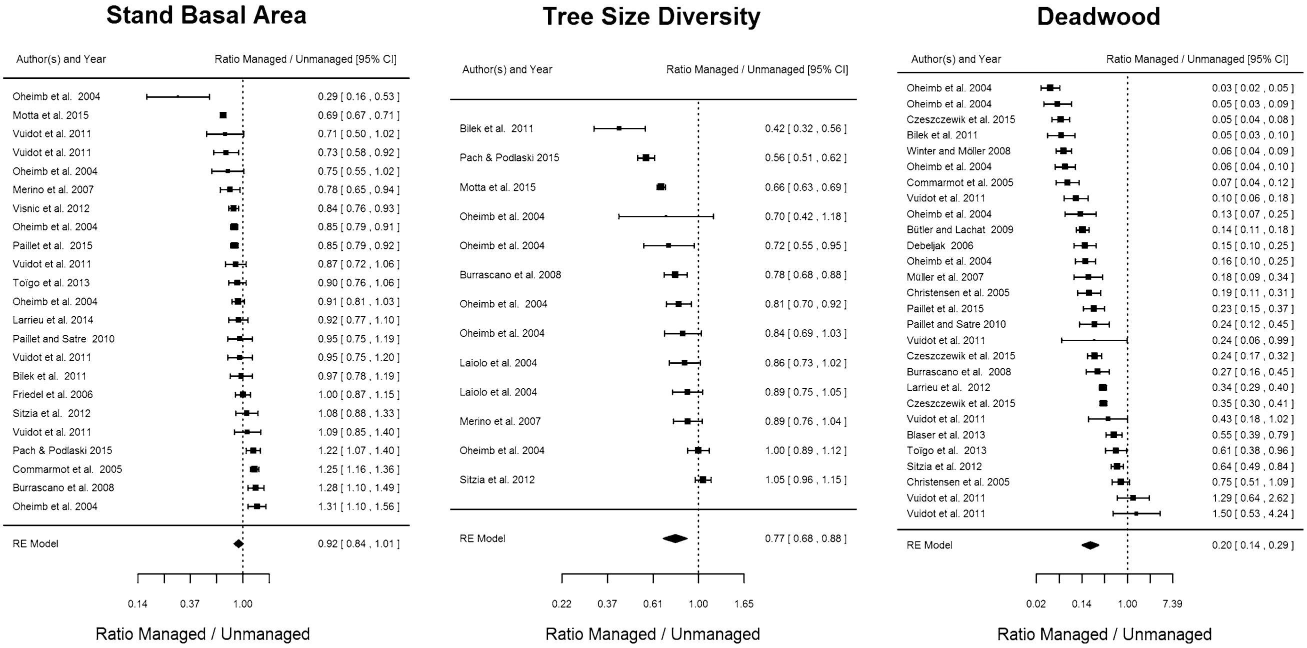

Fig. 3 Meta-analysis outcomes for selected structural traits: stand basal area, tree size diversity, and deadwood. Ratio managed/unmanaged is the delogarithmized effect size of Eq. 4. The *bottom line* shows the estimated overall effect size and its 95% CI as a rhomb. If this shape does not touch the *dashed 1.0-line*, this indicates a significant ($p < 0.05$) management effect. The *lines above* show the single comparison-wise results together with their CI

Table 5 Meta-analysis outcomes for all investigated structural traits

Category	*N*	*R*	95% CI		*p* value
Mean tree size	9	**0.79**	0.64	0.98	0.030
Stand basal area	23	0.92	0.84	1.01	0.072
Number of living trees	13	1.16	0.91	1.48	0.224
Maximum size	7	**0.54**	0.37	0.81	0.003
Number of microhabitats	7	**0.51**	0.36	0.72	<0.0001
Tree size diversity	13	**0.77**	0.68	0.88	<0.0001
Deadwood	28	**0.20**	0.14	0.29	<0.0001

N number of study results included, *R* estimated overall delogarithmized effect size (ratio managed/unmanaged), *95% CI* upper and lower bound of *R*'s 95% CI

Significant *R* values are printed in bold

measure for mixing effects, we compare the productivity of the mixed stand as a whole with the performance of pure stands of the same area proportions (see "Methodology" section and Pretzsch et al. 2017).

Figure 4 shows that all analysed species mixtures revealed the same pattern, as on trial level positive, neutral, or even negative mixing reactions were evident. Overall, the relative gain of productivity in mixed stands ranged between −29 and +153% depending on species combination with a clear tendency towards higher production in mixed stands. Thus, estimated overall delogarithmized effect sizes *R* (=ratio mixed/pure) showed significant positive deviations ($R > 1.0$) for the comparison between mixed and pure stands ($p \leq 0.05$). In detail, the mixture of oak and beech exceeded the productivity of the respective pure stands with $R = 1.24$, those of spruce and beech with $R = 1.19$ and the three species mixture fir/spruce/beech with $R = 1.20$.

Besides, the dataset also revealed with one exception (silver fir in the mixture Norway spruce/silver fir/European beech) that also at species level the mixture positively deviates on average from the productivity of the same species in the neighbouring pure stands. Our previous analyses along ecological gradients revealed the tendency that productivity gains by mixing are at maximum on poor sites, medium on mediocre sites, and lowest on fertile sites (Pretzsch et al. 2013a, b) which can explain part of the variation shown in Fig. 4. Thus, behind the seemingly contradictory findings about mixing effects on single comparison level may be simply differences in the environmental conditions.

The results so far were based on fully stocked pure and mixed stands and may be modified when thinning and small-scale disturbances are taken into consideration (Assmann 1970). To our knowledge, the data compiled from Fig. 4 are the most comprehensive in terms of primary or direct mixing effects.

Table 6 Meta-analysis outcomes for all investigated structural traits including time since abandonment of management (TSA) according to Eq. 3

Category	N	Intercept β_0 (±SE)	Slope β_1 (±SE)
Mean tree size	8	−0.040 ± 0.116	**−0.002** ± 0.001**
Stand basal area	21	−0.104 ± 0.085	0.001 ± 0.001$^{\text{n.s.}}$
Number of living trees	13	−0.214 ± 0.317	0.006 ± 0.005$^{\text{n.s.}}$
Maximum size	5	0.501 ± 0.407	**−0.018** ± 0.006**
Number of microhabitats	7	−0.508 ± 0.380	−0.004 ± 0.007$^{\text{n.s.}}$
Tree size diversity	11	−0.192 ± 0.197	0.000 ± 0.003$^{\text{n.s.}}$
Deadwood	24	−1.083 ± 0.391	−0.011 ± 0.007$^{\text{n.s.}}$

Significant values of the slope β_1 are printed in bold, significance level ** means $p < 0.01$

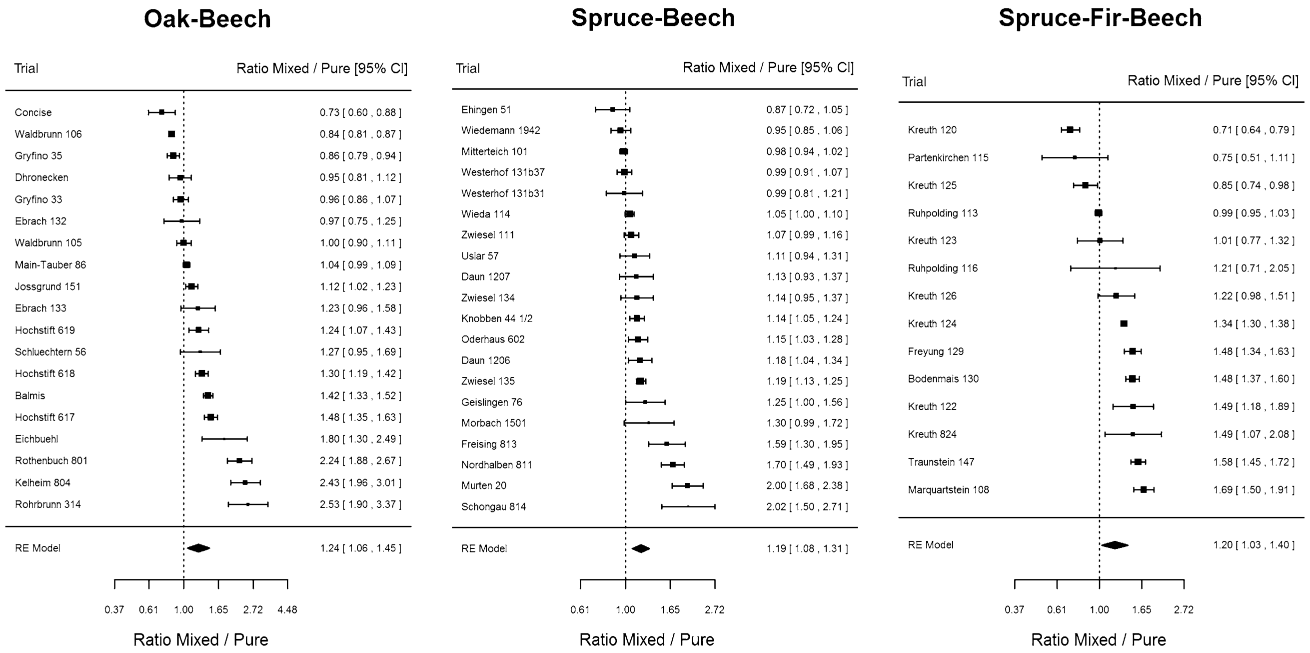

Fig. 4 Meta-analysis outcomes for productivity of mixed versus pure stands. Ratio mixed/pure is the delogarithmized effect size of Eq. 4. The *bottom line* shows the estimated overall effect size and its 95% CI as a rhomb. If this shape does not touch the *dashed 1.0-line*, this indicates a significant ($p < 0.05$) effect of species mixing on stand productivity. The *lines above* show the single comparison-wise results together with their CI

Discussion

Biodiversity and ecosystem functioning in relation to forest management

Species diversity (composition)

The compositional aspect of biodiversity according to Noss (1990) reflects the occurrence and abundance of organisms within the taxonomic level of interest. In general, species richness and species diversity vary between ecosystems and biomes. A major driving factor for this variation is represented by variation in environmental conditions, whereas, in temperate climates, the diversity–productivity relation follows mainly a unimodal optimum curve (Zobel and Pärtel 2008). Species diversity in Central European forest ecosystems depends on the stability of biogeophysical factors in a given region. Recurring disturbances like periodical fires may cause fluctuations in the composition of functional groups, thereby altering the status of diversity (Moretti et al. 2006; Schnitzler and Borlea 1998). The same forest ecosystems may reveal different levels of species composition depending on the successional status after disturbances (von Oheimb et al. 2007; Smith and Smith 2009). Forest stand management may interact with species diversity in various respects. In Central Europe's forests, a broad variety of silvicultural concepts are found ranging from age class plantation systems using alien tree species to close-to-nature forestry attempting to mimic natural forest dynamics. Clearly, such different concepts lead to different levels of impact of forest stand management on species diversity triggered directly by changing tree species composition, successional status and structural characteristics.

In comparing managed and unmanaged forests, a holistic view on species diversity including all faunal and floral taxa is virtually impossible. Most studies dealing with species diversity in managed and unmanaged forests therefore focus on selected taxa of plants, fungi, bryophytes, lichens, or animals, functional groups of species, e.g. carnivorous, phytophagous omnivorous ground beetles cf. Toïgo et al. (2013), or habitats, e.g. soil, stems, tree crowns.

Structural diversity

Structural diversity displays high relevance in the frame of biodiversity. According to McElhinny et al. (2005) it mainly provides two key functions: First, forest characteristics deliver a basis for identification of habitat and key structures. Second, high variability or abundance of structures generally equals high diversity of species and plants. While past research has mainly focused on the former point, more and more studies have established links between structural attributes and taxonomic biodiversity (Brändle and Brandl 2001; Winter and Möller 2008; Müller et al. 2009, 2014).

Forest stand management primarily impacts on the following structural attributes: tree size and age distribution and variation, stand density, microhabitats, and deadwood availability. Tree age, stem diameter at breast height (dbh), stem height, basal area or stand density are basic parameters to describe stand structure in its entirety (Pretzsch 1997) and are commonly collected by recurrent forest inventories. Beside their direct importance for stand management, these values are known to correlate in their absolute magnitude with measures like species richness, habitat abundance, or other biodiversity indicators (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Jacob et al. 2013). For instance, the number of species inhabiting a tree or particular habitat qualities increase with dbh (Friedel et al. 2006), and deadwood quantity is positively correlated with wood-living fungal or saproxylic beetle species richness (Gao et al. 2015). But also their relative characteristics, within the literature often reported as diameter and height diversity (McElhinny et al. 2005; Motz et al. 2010), are important indicator variables. According to the 'habitat heterogeneity hypothesis' (cf. Tews et al. 2004), an increased structural variability leads to an increase in habitats and therefore to an increase in species richness and diversity. A varying number of structures are equal to a large number of niches and environmental resources. The same applies for measures of tree microhabitats and deadwood. Microhabitats are specific structures on trees, such as cavities, bark pockets, broken branches or others, and are highly interlinked with the abundance of many taxonomic species (Michel and Winter 2009; Winter and Möller 2008). In particular, the amount of deadwood is a crucial component in forest ecosystems as a host for flora and fauna richness and as it guarantees ecosystem functions (Grove 2002; Larrieu et al. 2014). However, in contrast to diversity indicators, those can be used as surrogates for specific habitats and hence distinct species or species groups (Brändle and Brandl 2001; Ulyshen 2011; Gao et al. 2015).

Ecosystem functioning and biodiversity

Ecosystem functioning is an important but not yet adequately considered feature strongly connected to biodiversity (e.g. Hooper et al. 2005). By ecosystem functioning on stand level, e.g. the biomass production, nutrient cycling, and natural stand regeneration is addressed. While the stand composition and structure (at forest stand level and during a stand's life) are commonly used aspects for monitoring, quantifying and indicating as well as ranking of biodiversity, ecosystem functioning is an often neglected aspect of biodiversity (cf. Noss 1990).

Functioning certainly has strong feedbacks with biodiversity: the amount of biomass produced per unit area and time, for example, determinates the food supply and existence of the fauna, while the quality and quantity of cycling nutrients affect the flora (Foster and Bhatti 2002). The natural regeneration process contributes to ecosystem persistence. Besides, contradictory views exist about the diversity–productivity relation. According to Srivastava and Lawton (1998) and Potter and Woodall (2014), there is evidence that more productive sites positively alter species richness, whereas Zobel and Pärtel (2008), as mentioned above, argue that in temperate climates the diversity-productivity-relation follows mainly a unimodal optimum curve (Zobel and Pärtel 2008).

Biomass and volume productivity is a core indicator of ecosystem functioning at stand level. Productivity of trees makes up to 80–90% of the primary productivity in temperate forests (Larcher 2003). The long-term performance of a stand in terms of matter production represents more than just the potential harvest volume: It reflects the site fertility, the potential primary production which serves all other community members as nutrition, and it determinates the annual turnover which is essential for soil formation or water storage (Assmann 1970; Pretzsch 2009).

When we consider the effect of management on biodiversity, also the effect of management on productivity has to be taken into account. There are many different aspects

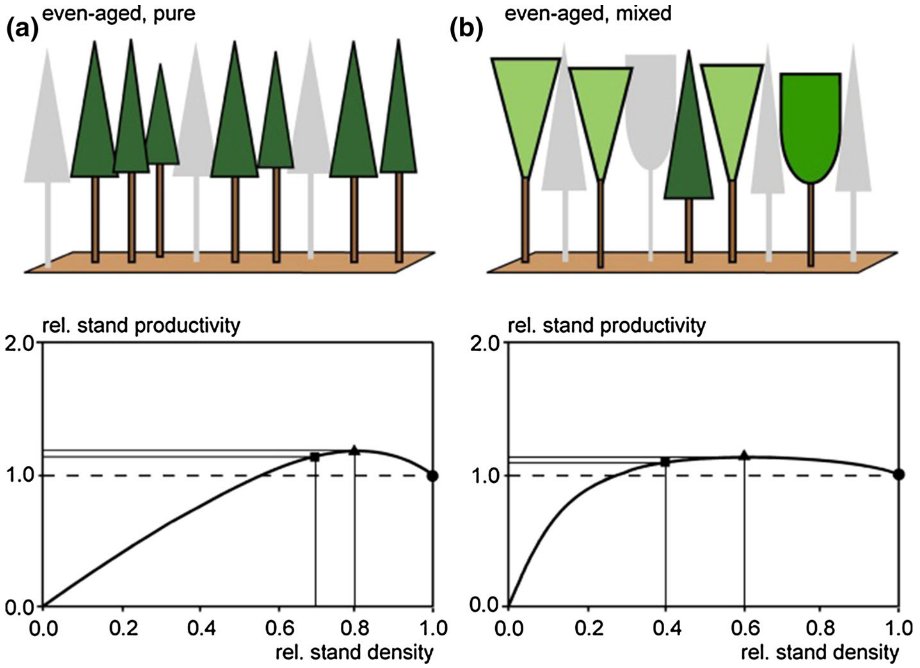

Fig. 5 Stand growth can be higher in moderately thinned than in unmanaged and the growth resilience can be more pronounced in mixed compared with pure stands. Schematic representation of the stand structure (*above*) and the stand density–productivity relationship (*below*). The course of the curve can be quantified by the origin (*filled circle* both relative density and productivity = 1.0), the culmination point of the curve (*filled triangle*), and the point of critical density (*filled square*) where the productivity losses arrive at 5% of the maximum stand productivity

of stand management that effect stand productivity as component of biodiversity, for instance species mixing, thinning, natural stand regeneration, and fertilization (Assmann 1970). Other interference by management as the application of pesticides, pruning or others are treated just briefly as they are less relevant in Central Europe or already covered by the main effects.

A high productivity alone is not necessarily beneficial for biodiversity. For example, a Norway spruce plantation on a fertile site can be highly productive (if disturbances stay away), but poor in biodiversity due to shortage of compositional and structural elements. Subsequently, we focus on the effect of thinning and tree species mixing on stand productivity. From our point of view, mixing is an actively promoted silvicultural treatment compared to the formerly preferred monocultures.

Species mixing affects the ecosystem biodiversity in manifold ways: different tree species contribute directly to the species diversity because of their holobiontic dependants as, e.g. small mammals, birds, lichens, miroorganisms (Cavard et al. 2011). Mixing also often increases structural heterogeneity and productivity (Dieler and Pretzsch 2013, 2014; Morin et al. 2011; Pretzsch 2014; Pretzsch and Schütze 2008; Vandermeer 1989; Zhang et al. 2012). In addition, it may have an effect on persistence of structure and productivity by reduction of risk (Griess and Knoke 2011; Griess et al. 2012; Knoke et al. 2005).

As the unimodal relationship between growth and stand density achieved the status of a general rule by Assmann's (1970) extensive analyses, we refrain from redoing a meta-analysis (see also overarching analysis by Pretzsch 2005b). The relationship between stand density and productivity as shown in Fig. 5 is most relevant as silvicultural interference primarily means stand density reduction. In temperate forests, there is a unimodal relationship between stand density and productivity which may have a different course in homogeneous compared with heterogeneous stands (Fig. 5a, b). The two density growth relationships are unimodal, i.e. with lowest productivity level at low densities, increasing productivity when stand density increases, and a slight decrease in productivity when approaching maximum stand density. However, while the patterns are similar in principle, the position and extent of the curves' saddle is rather different.

In the schematic example (Fig. 5a) a maximum relative productivity of $rp_{max} = 1.25$ (i.e. 125% of the productivity in fully stocked pure stands) is achieved at a relative stand density of $rd_{max} = 0.80$ (i.e. 20% below the maximum stand density). The critical relative density where only 95% of the maximum productivity are achieved (i.e. density reduction causes a productivity loss of 5%) amounts to $rd_{crit} = 0.7$. With other words, maximum productivity can be assumed not for maximum but below-maximum stand density conditions (Assmann 1970, pp. 227–235).

In contrast, in the mixed stand (Fig. 5b), a relative stand productivity of $rp_{max} = 1.20$ is achieved at a relative density of $rp_{max} = 0.60$. The critical stand density causing productivity losses of 5% amounts to $rd_{crit} = 0.4$. The relative density and productivity of both the maximum productivity and critical productivity characterize growth resilience with is relevant for system understanding and regulation (Mitscherlich 1948, 1975; Pretzsch 2005a, b).

Interpretation of the meta-analysis' results

Mainly moderate effects of silviculture on the three components of biodiversity

The studies included in our meta-analyses revealed that differences between managed and unmanaged forest stands in Central Europe in terms of species richness and species diversity are not distinct in general. This view is also supported by other studies that could not be included into the meta-anaylses due to missing indication of mean and SD values. For example, Müller et al. (2007) report lower diversity of wood-inhabiting fungi in managed forests, while no negative effect of forest management on the diversity of soil fungi was found by Wubet et al. (2012). Higher diversity in managed forest was observed for bats (Obrist et al. 2011), herb vegetation (Brunet et al. 1996), and ground-dwelling beetles (Lange et al. 2014). Opposite effects of management on the diversity of epiphytic and dead wood-dwelling lichens have been described by Nascimbene et al. (2013).

Obviously, however, differences in certain structural traits seem to be triggered by forest management leading to a reduced or at least altered structural diversity in managed forest stands compared to unmanaged ones. This effect was the stronger, the longer ago forest management had been abandoned in the unmanaged stands. Assuming that a reduced structural diversity leads to a lower provision of habitats, we might also assume that in managed forest stands the composition of functional groups is also modified (e.g. Sabatini et al. 2010) but not necessarily species diversity in general (e.g. Toïgo et al. 2013; Gossner et al. 2013). The situation may become more complex when moving from the stand level to larger scales (which is not the focus of this study): silvicultural interventions leading to a broad range of microclimatic conditions on the landscape scale (e.g. by applying the shelterwood system) can harbour higher biodiversity than selection systems resulting in high within but low between stand heterogeneity (Schall et al. 2017). Gossner et al. (2014) also pointed out that single structural stand characteristics have weak explanatory power for overall species diversity, while they rather have, if the diversity of subgroups is considered. This might well explain our outcome that management significantly changes stand structure but not compositional features.

Positive interactions between components of biodiversity point the way for silviculture

Silvicultural measures, which aim at improving biodiversity by enhancing positive interactions between two or more components of biodiversity, are of special interest. This applies, e.g. for the relationship between tree species richness and stand productivity. Worldwide the depletion of tree species richness should be stopped as it is the main cause for a loss of forest productivity (Naeem et al. 2012). In regions like Central Europe, where forestry has replaced mixed forests by monocultures in the past (Pretzsch 2005a), the biodiversity–productivity relationship (BPR) shows the potential of increasing productivity by transition from monocultures to mixed-species stands. This is one reason, why presently many stand management guidelines strive for assemblages of at least 2–3 species when establishing new and regulating existing forest stands (see, e.g. Bayerische Staatsforsten 2015).

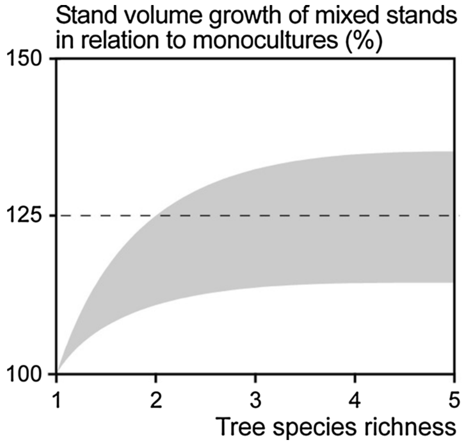

Fig. 6 Degressive increase in the stand productivity with increasing tree species richness in temperate forests (schematic representation taken from Pretzsch 2016, also according to Liang et al. 2016). This productivity increase effect is enhanced by species complementarity through niche efficiency (Liang et al. 2016; Pretzsch et al. 2013a, b). The shaded area shows maximum overyielding of 35% or just 15% if very complementary species or very similar species are mixed, respectively. In contrast to subtropical or tropical regions data from stands with more than five species are rare in Central Europe

Several individual studies showed that stand productivity increases degressively with species richness (Paquette and Messier 2011; Pretzsch 2013; Ruiz-Benito et al. 2014). This productivity increase effect is enhanced by species complementarity through niche efficiency (Liang et al. 2016; Pretzsch et al. 2013a, b). The most comprehensive study of the BPR by Liang et al. (2016) was based on forest inventories from 777,126 permanent sample plots that contain more than 3,000,000 trees from 8325 species and cover most of the global terrestrial biomes. At landscape, country, ecoregion, and global level, this study found a degressively increasing BPR as shown in Fig. 6. Liang et al. (2016) stress that globally a 10% loss of tree species richness corresponded on average to a 6–7% decline in productivity and the rate of this decline increased exponentially with further reduction of tree species diversity. However, those findings also encourage the transformation of monocultures into two- or three-specie polycultures that presently is promoted especially in Europe but also in many other parts of the world, where monocultures dominate. So, turning away from monocultures has the potential to increase both, species (at least tree species) richness and diversity as well as forest productivity and functioning.

In this context Verschuyl et al. (2008) found a positive correlation between stand structure and bird diversity modified by site quality. Site quality was quantified by the available radiation and other factors related to primary productivity such as water and nutrient supply. They show that the relation between (bird) species richness and available energy is an optimum curve with lower diversity at the extremes and an optimum in between. This could be confirmed across the northwestern USA, however, on landscape level, due to a narrower spectrum of available energy, only parts of this optimum curve can be detected. In energy-limited landscapes, the relation between species richness and energy was positive or hump-shaped, and, in contrast, flat or negative in energy-rich landscapes. However, in energy-rich-landscapes, forest structure explained more of the variations in bird diversity richness. Similar trends are reported from Goldmann et al. (2015) who found lower diversity in fungal operational taxonomic units in unmanaged beech stands on a higly productive site than on a mediocre site. This implies that strategies for enhancing biodiversity in forest landscapes should depend on the conditions of energy supply. In energy-rich landscapes disturbances like thinnings can increase forest diversity effectively by breaking the competitive dominance of a few plant species. Thus, structure-creating thinnings on landscape level are likely to enhance bird diversity in high-energy environments. In comparably poor landscapes where structure is not such a strong driver for diversity, Verschuyl et al. (2008) consider such area-wide measures not as effective. They recommend to concentrate structure-creating management on local high-energy hotspots and to base harvest decisions from other considerations in the remaining places.

Ishii et al. (2004) review works from a north American and a Japanese canopy research site, each in a temperate natural forest, in order to scrutinize relationships among canopy structure, stand productivity and biodiversity. The authors point out that the diversity of canopy-dwelling organisms clearly increases with more complex three-dimensional canopy structures in a stand. Concerning the trade-off between diversity and productivity they argue that complex canopy structures lead to a more pronounced niche differentiation among tree species which in turn increases stand productivity.

As a consequence, thinnings, which can be seen as artificial disturbances of stand structure do not impair and might even enhance biodiversity in some regards, although our results show that they may have a homogenizing effect on stand structure. However, a positive effect of thinnings on biodiversity seems to be most pronounced on productive sites and least on poor sites. Thus, management for biodiversity is more promising on good sites because here, stand structure is more closely linked to biodiversity. In mixed stands, productivity is much less affected by thinning. This means that in mixed stands there are more options for enhancing diversity by creating structure without losing production than in pure stands. However, and this is an actual trade-off, overyielding effects by tree species mixture are most pronounced on poor sites, while on good sites even underyielding may occur.

Indirect effects even less known than direct effects

All included studies concentrated on the direct effect of silviculture on the components of biodiversity. By direct effects of silvicultural interference on stand productivity, we reflect those effects which are always and inherently coupled with a silvicultural operation (species mixing, thinning, natural regeneration, fertilization). For example, mixing of tree species with complementary ecological traits directly causes competition reduction, facilitation, and overyielding. Heavy thinning from above causes temporary growth reduction due to the release of future crop trees. Natural regeneration buffers growth losses due to temporary clearing by maintaining a continuous forest cover (Pretzsch et al. 2015a, b). Indirect effects of silvicultural treatment, in contrast, may have effect in future depending on possibly changing environmental conditions. For instance, mixing of adapted species may stabilize and increase productivity compared with pure stands under climate change (Thurm et al. 2016). Thinning may increase the mechanical stem stability and avoid tree and productivity losses due to windthrow or snow damage. Natural regeneration under overstory may prevent treeless phases and several years' productivity in case of loss of the overstory by bark beetle or storm damage. Beyond the temporary pulse of resources and growth, fertilization may cause a sustainable improvement in resource supply and resource storage capacity and productivity of previously poor and low-growing ecosystems. Notice, that the indirect effects are even less known and predictable than the here addressed direct effects.

Conclusions

Our results emphasize that forest management per se not necessarily has a negative impact on biodiversity. The contrasting results of the included studies rather require a more comprehensive view when evaluating management activities in the frame of biodiversity. Diversity of species, structural traits and functions need to be addressed as well as the specific impact of the applied silvicultural system in particular on forest structure has to be taken into account. In this context Brunet et al. (2010) describe the sensitivity of different functional groups on different silvicultural concepts for the management of beech forests in Europe. In terms of classifying the intensity of forest management activities more generally Schall and Ammer (2013) provide a promising approach.

Although we focussed on forest stand level and did not consider the patchiness of forest stands and its effect on biodiversity on landscape level (cf. Wells et al. 2011), our results contribute to the open debate, whether segregative forestry or integrative approaches aiming at 'close-to-nature' forestry better promotes biodiversity issues. This is a relevant question as biodiversity is one important component of a broad set of ecological, economical, and socioeconomical forest functions and services. A segregative approach may promote various functions and services on the expense of others, better fulfilled by an integrative approach. So, it is of high interest, how the integrative approach, which considers humans and their disturbances as part of a system comes off in terms of biodiversity maintenance compared with the unmanaged forest resulting from a segregative concept.

In summary, we conclude that biodiversity (species composition, structure, functioning) changes only moderately from unmanaged to managed forests as long as also the anthropogenic disturbances inferred by management remain moderate, e.g. when applying the selection forest, shelterwood, or femel-coupe system. One reason for this might be that the unmanaged stands in the analysed studies often constitute a questionable reference; often they were managed in the past and they still are directly or indirectly influenced by anthropogenic impacts such as climate change, dry deposition, browsing due to predator elimination. Beyond the actual scope of this study, on larger spatial units than single stands, gamma diversity can be promoted by different silvicultural regimes that create high within-stand heterogeneity on the landscape scale (Schall et al. 2017). In contrast, many unmanaged forest in Central Europe, which were only recently set aside, tend to become more homogenous for at least some decades unless disturbances create substantial structural heterogeneity.

Furthermore, disturbances like fires, bark beetle infestations, or storm damages were and still are mostly prevented or mitigated even in unmanaged forests in order to protect humans and their property, but are drivers for biodiversity in many forest ecosystems (Beudert et al. 2015). Thus, many of the included unmanaged forests lack large scale disturbances.

The differences between managed and unmanaged forests are also vague, as disturbances by silvicultural treatment are important for creating heterogeneous structures and habitats. Modern silviculture emulates natural disturbances, e.g. by femel, or selection coupes in the lowland forests, or gap coupes in the mountain forests. So, the differences get blurred, as unmanaged forests are hardly pristine and managed forests tend towards close-to-nature approaches.

In densely populated regions like Central Europe really pristine, unmanaged forests are hardly to find for both, science and conservation. And it may be argued, that humans are part of ecosystems in this area since millennia and a segregative management approach might be unrealistic and unreasonable. Advantages of the integrative approach are the need for integration, participation, understanding the needs of all forest users, including plants, animals, fungi, microbes, and humans. Certainly, integration requires enhanced knowledge about the biodiversity–management relationship at the stand and higher levels of organization. This is relevant for the design of multipurpose forests that may be expressed by various management strategies like retention forestry (Mori and Kitagawa 2014), selection systems or reduced impact selective logging (Chaudhary et al. 2016). Understanding and sustainably using all the values forest ecosystems provide may contribute to a higher appreciation and responsible and cautious forest stewardship.

Acknowledgements We wish to thank the Bavarian State Forest Enterprise (Bayerische Staatsforsten AöR) for providing funds for the literature review and the Bavarian State Ministry for Nutrition, Agriculture and Forestry for permanent support of the project W 07 "Long-term experimental plots for forest growth and yield research". Thanks are also due to the reviewers for their constructive criticism and helpful comments on the manuscript.

References

Abetz P, Mitscherlich G (1969) Überlegungen zur Planung von Bestandesbehandlungsversuchen. Allg Forst Jagdztg 150:175–178

Assmann E (1970) The principles of forest yield study. Pergamon Press, Oxford, p 506

Bayerische Staatsforsten (2015) Silvicultural guidelines for various forest tree species and stand types. http://www.baysf.de/de/wald-verstehen/waldbau.html

Beudert B, Bässler C, Thorn S, Noss R, Schröder B, Dieffenbach-Fries H, Foullois N, Müller J (2015) Bark beetles increase biodiversity while maintaining drinking water quality. Conserv Lett 8(4):272–281

Biber P, Borges JG, Moshammer R, Barreiro S, Botequim B, Brodrechtová Y, Brukas V, Chirici G, Cordero-Debets R, Corrigan E, Eriksson LO, Favero M, Galev E, Garcia-Gonzalo J, Hengeveld G, Kavaliauskas M, Marchetti M, Marques S, Mozgeris G, Navrátil R, Nieuwenhuis M, Orazio C, Paligorov I, Pettenella D, Sedmák R, Smreček R, Stanislovaitis A, Tomé M, Trubins R, Tuček J, Vizzarri M, Wallin I, Pretzsch H, Sallnäs O

(2015) How sensitive are ecosystem services in European forest landscapes to silvicultural treatment? Forests 2015(6):1666–1695

Brändle M, Brandl R (2001) Species richness of insects and mites on trees: expanding Southwood. J Anim Ecol 70:491–504

Brunet J, Falkengren-Grerup U, Tyler G (1996) Herb layer vegetation of south Swedish beech and oak forests—effects of management and soil acidity during one decade. For Ecol Manag 88:259–272

Brunet J, Fritz Ö, Richnau G (2010) Biodiversity in European beech forests—a review with recommendations for sustainable forest management. Ecol Bull 53:77–94

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. For Ecol Manag 291:458–479

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA et al (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Cavard X, Macdonald SE, Bergeron Y, Chen HYH (2011) Are mixedwoods important for biodiversity conservation: evidence for understory plants, songbirds, soil fauna and ectomycorrhizae in boreal and northern temperate forests. Environ Rev 19:142–161

Chaudhary A, Burivalova Z, Koh LP, Hellweg S (2016) Impact of forest management on species richness: global meta-analysis and economic trade-offs. Nat Sci Rep 6:23954. doi:10.1039/srep23954

Convention on Biological Diversity (2010) Strategic plan for biodiversity 2011–2020 and the Aichi targets. Secretariat of the Convention on Biological Diversity, Montreal. https://www.cbd.int/decision/cop/?id=12268. Accessed July 2016

Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. For Ecol Manag 295:97–108

Dieler J, Pretzsch H (2014) Plastizität von Baumkronen: strukturmerkmale von Fichten und Buchen im Rein- und Mischbestand. Allg Forst Jagdztg 184(11/12):247–262

Duelli P, Obrist MK (2003) Biodiversity indicators: the choice of values and measures. Agric Ecosyst Environ 98(1):87–98

Elbakidze M, Angelstam P, Sobolev N, Degerman E, Andersson K, Axelsson R, Hojer O, Wennberg S (2013) Protected area as an indicator of ecological sustainability? A century of development in Europe's boreal forest. Ambio 42:201–214

FAO (2010) Global forest resource assessment 2010. FAO Forestry Paper 163. Food and Agriculture Organization of the United Nations, Rome

Forest Europe (2011) State of Europe's forests. In: Ministerial conference on the protection of forests in Europe, Oslo. http://www.foresteurope.org/full_SoEF. Accessed July 2016

Foster NW, Bhatti JS (2002) Forest ecosystems: nutrient cycling. In: Lal R (ed) Encyclopedia of soil science, vol 1. Dekker, New York, pp 718–720

Friedel A, Dengler J, Härdtle W (2006) Species diversity and species composition of epiphytic bryophytes and lichens–a comparison of managed and unmanaged beech forests in NE Germany. Feddes Repert 117(1–2):172–185

Gao T, Nielsen AB, Hedblom M (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol Ind 57:420–434

Goldmann K, Schöning I, Buscot F, Wubet T (2015) Forest management type influences diversity and community composition of soil fungi across temperate forest Ecosystems. Front Microbiol 6:1300. doi:10.3389/fmicb.2015.01300

Gossner MM, Lachat T, Brunte J, Isacsson G, Bouget C, Brustel H, Brandl R, Weisser WW, Müller J (2013) Current near to nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conserv Biol 27(3):606–614

Gossner MM, Schall P, Ammer C, Ammer U, Engel K, Schubert H, Simon U, Utschick H, Weisser WW (2014) Forest management intensity measure as alternative to stand properties for aquantifying effects on biodiversity. Ecosphere 5(9):113. doi:10.1890/ES14-00177.1

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: proceudres and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Griess VC, Knoke T (2011) Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Can J For Res 41(1141–1158):2011

Griess VC, Acevedo R, Härtl F, Staupendahl K, Knoke T (2012) Does mixing tree species enhance stand resistance against natural hazards? A case study for spruce. For Ecol Manag 267(284–296):2012

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Hannah L, Midgley GF, Lovejoy T, Bond WJ, Bush MLJC, Lovett JC, Woodward FI (2002) Conservation of biodiversity in a changing climate. Conserv Biol 16(1):264–268

Hedges LV, Gurevitch J, Curtis P (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hobi ML, Commarmot B, Bugmann H (2015) Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). J Veg Sci 26(2):323–336

Hooper DU, Chapin FS, Ewe 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) Effect of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35. doi:10.1890/04-0922

Hunter ML (1999) Biological diversity. In: Hunter ML (ed) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, pp 3–21

Ishii HT, Tanabe S, Hiura T (2004) Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. For Sci 50(3):342–355

Jacob M, Bade C, Calvete H, Dittrich S, Leuschner C, Hauck M (2013) Significance of over-mature and decaying trees for carbon stocks in Central European natural sprcue forests. Ecosystems 16:336–346

Knoke T, Stimm B, Ammer C, Moog M (2005) Mixed forests reconsidered: a forest economics contribution on an ecological concept. For Ecol Manag 213:102–116

Lange M, Türke M, Pačalić E, Boch S, Hessenmöller D, Müller J, Prati D, Socher SA, Fischer M, Weisser WW, Gossner MM (2014) Effects of forst management on ground-dwelling beetles (Coleoptera; *Carabidae*, *Staphylinidae*) in Central Europe are mainly mediated by changes in forest structure. For Ecol Manag 329:166–176

Larcher W (2003) Physiological plant ecology, 4th edn. Springer, Berlin

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. Can J For Res 42:1433–1445

Larrieu L, Cabanettes A, Brin A, Bouget C, Deconchat M (2014) Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. Eur J For Res 133:355–367

Larsson TB (2001) Biodiversity evaluation tools for European forests. In: Franc A, Laroussinie O, Karjalainen T (eds) EFI proceedings of criteria and indicators for sustainable forest management at the forest management unit level, Nancy, France, vol 38

Liang J, Crowther ThW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, De Miguel S, Paquette A, Hérault B, Scherer-Lorenzen M, Barrett ChB, Glick

H, Hengeveld GM, Nabuurs G-J, Pfautsch S, Viana H, Vibrans AC, Ammer Ch, Schall P, Verbyla D, Tchebakova N, Fischer M, Watsan JV, Chen H, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Eljatib ChS, Lee E, Lee B, Kim H-A, Bruelheide H, Coomes DA, Piotto D, Sunderland T, Schmid B, Rautiainen M, Gourlet-Fleury S, Sonké B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto Ch, Frizzera L, Balazy R, Oleksyn J, Zawila-Niedzwiecki T, Bouriaud O, Bussotti F, Finér L, Jaroszewicz B, Jucker T, Valladares F, Jagodzinski AM, Luis PP, Gonmadje Ch, Marthy W, O'Brien T, Martin EH, Marshall A, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier Frédéric, Wortel V, Obiang NE, Ferreira LV, Odeke DE, Vasquez RM, Reich PB (2016) Positive biodiversity-productivity relationship predominant in global forests. Science. doi:10.1126/science.aaf8957

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, p 351

Lindenmayer DB, Noss RF (2006) Salvage logging, ecosystem processes, and biodiversity conservation. Conserv Biol 20(4):949–958

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: its definition and measurement. For Ecol Manag 218:1–24

McGinley M, Ellis E, Lloyd J (2011) Biome. In: Cleveland CJ (ed) Encyclopedia of earth. Environmental Information Coalition, National Council for Science and the Environment, Washington [First published in the Encyclopedia of Earth November 7, 2008; Last revised Date September 27, 2011]. www.eoearth.org/article/Biome?topic=58073. Accessed April 2013

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. For Ecol Manag 257:1453–1464

Mitscherlich EA (1948) Die Ertragsgesetze. Akademie-Verlag, Berlin

Mitscherlich G (1975) Wald, Wachstum und Umwelt. JD Sauerländer's Verlag, Frankfurt am Main

Moretti M, Duelli P, Obrist MK (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149:312–327

Mori AS, Kitagawa R (2014) Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: a global meta-analysis. Biol Conserv 175:65–73

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between niches. Ecol Lett. doi:10.1111/j.1461-0248.2011.01691.x

Motz K, Sterba H, Pommerening A (2010) Sampling measures of tree diversity. For Ecol Manag 260:1985–1996

Müller J, Engel H, Blaschke M (2007) Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. Eur J For Res 126:513–527

Müller J, Pöllath J, Moshammer R, Schröder B (2009) Predicting the occurrence of Middle Spotted Woodpecker Dendrocopos medius on a regional scale, using forest inventory data. For Ecol Manag 257:502–509

Müller J, Jarzabek-Müller A, Bussler H, Gossner MM (2014) Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Anim Conserv 17(2):154–162

Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. Science 336:1401–1406

Nascimbene J, Dainese M, Sitzia T (2013) Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. For Ecol Manag 2013:325–332

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4(4):355–364

Obrist MK, Rathey E, Bontadina F, Martinoli A, Conedera M, Christe P, Moretti M (2011) Response of bat species to sylvo-pastoral abandonment. For Ecol Manag 261:789–798

Paillet Y, Bergès L et al (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24(1):101–112

Paquette A, Messier C (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob Ecol Biogeogr 20:170–180

Parviainen J, Bucking W, Vandekerkhove K, Schuck A, Paivinen R (2000) Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). Forestry 73:107–118

Potter KM, Woodall CW (2014) Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. For Ecol Manag 321:117–129

Pretzsch H (1997) Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. For Ecol Manag 97:237–253

Pretzsch H (2005a) Diversity and productivity in forests. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function. Ecol Studies 176. Springer, Berlin, pp 41–64

Pretzsch H (2005b) Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). Evidence from long-term experimental plots. Eur J For Res 124:193–205

Pretzsch H (2009) Forest dynamics, growth and yield. Springer, Berlin

Pretzsch H (2013) Facilitation and competition in mixed-species forests analysed along an ecological gradient. Nova Acta Leopold 114(391):159–174

Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For Ecol Manag 327:251–264

Pretzsch H (2016) Ertragstafel-Korrekturfaktoren für Umwelt- und Mischungseffekte. AFZ-DerWald 14(2016):47–50

Pretzsch H, Schütze G (2008) Trangressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. Eur J For Res. doi:10.1007/s10342-008-0215-9

Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel J, Spellmann H, Zingg A (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann For Sci 67:712

Pretzsch H, Bielak K, Block J, Bruchwald A, Dieler J, Ehrhart HP, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A (2013a) Productivity of mixed versus pure stands of oak (*Quercus pretraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. Eur J For Res 132(2):263–280

Pretzsch H, Bielak K, Bruchwald A, Dieler J, Dudzinska M, Ehrhart HP, Jensen AM, Johannsen VK, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A (2013b) Mischung und Produktivität von Waldbeständen. Ergebnisse langfristiger ertragskundlicher Versuche. Allg For Jagdztg 184(7/8):177–196

Pretzsch H, del Río M, Ammer C, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Dirnberger G, Drössler L, Fabrika M, Forrester D, Godvod K, Heym M, Hurt V, Kurylyak V, Löf M, Lombardi F, Matovic B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Schütze G, Schweig J, Skryszewski J, Sramek V, Sterba H, Stojanovic D, Svoboda M, Vanhellemont M, Verheyen K, Wellhausen K, Zlatanov T, Bravo-Oviedo A (2015a) Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L) analysed along a productivity gradient through Europe. Eur J For Res 134(5):927–947

Pretzsch H, Biber P, Uhl E, Dauber E (2015b) Long-term stand dynamics of managed spruce-fir-beech mountain forests in Central Europe: structure, productivity and regeneration success. Forestry 88(4):407–428

Pretzsch H, Forrester DI, Bauhus J (2017) Mixed-species forests. Ecology and management. Springer, Berlin, 653 p

Püttmann KJ, Coates KD, Messier C (2009) A critique of silviculture: managing for complexity. Island Press, Washington, p 200

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Ruiz-Benito P et al (2014) Diversity increases carbon storage and tree productivity in Spanish forests. Glob Ecol Biogeogr 23:311–322

Sabatini FM, Burrascano S, Blasi C (2010) Niche heterogeneity and old growth forests conservation value. Ital J For Mt Environ 65(5):621–636

Schall P, Ammer C (2013) How to quantify forest management intensity in Central European forests. Eur J For Res 132:379–396

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Jung K, Baumgartner V, Blaser S, Böhm S, Buscot F, Daniel R, Goldmann K, Kaiser K, Kahl T, Lange M, Müller J, Overmann J, Renner SC, Schulze E-D, Sikorski J, Tschapka M, Türke M, Weisser WW, Wemheuer B, Wubet T, Ammer C (2017) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. J Appl Ecol. doi:10.1111/1365-2664.12950

Schnitzler A, Borlea F (1998) Lessons from natural forests as keys for sustainable management and improvment of naturalness in managed broadleaved forests. For Ecol Manag 109:293–303

Schwappach A (1893) Wachstum und Ertrag normaler Rotbuchenbestände. Springer, Berlin, p 104

Shannon CE, Weaver W (1949) The mathematical theory of communication. The University of Illinois Press, Urbana, p 117

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

Sitzia T, Trentanovi G, Dainese M, Gobbo G, Lingua E, Sommacal M (2012) Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. For Ecol Manag 270:232–238

Smith TM, Smith RL (2009) Ökologie. German translation “Elements of ecology”. Pearson Education Deutschland GmbH

Spellerberg IF, Fedor PJ (2003) A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the ‘Shannon-Wiener’ Index. Glob Ecol Biogeogr 12(3):177–179

Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am Nat 152:510–529

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. J Biogeogr 31:79–92

Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. For Ecol Manag 376:205–220

Toïgo M, Paillet Y, Noblecourt T, Soldati F, Gosselin F, Dauffy-Richard E (2013) Does forest management abandonment matter more than habitat characteristics for ground beetles? Biol Conserv 157:215–224

Ulyshen MD (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. For Ecol Manag 261(9):1479–1489

Vandermeer J (1989) The ecology of intercropping. Cambridge University Press, Cambridge

Verschuyl JP, Hansen AJ, McWethy DB, Sallabanks R, Hutto RL (2008) Is the effect of forest structure on bird diversity modified by forest productivity? Ecol Appl 18(5):1155–1170

Verschuyl J, Riffell S, Millerc D, Wigley TB (2011) Biodiversity response to intensive biomass production from forest thinning in North American forests—a meta-analysis. For Ecol Manag 261:221–232

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36(3):1–48

von Oheimb G, Friedel A, Bertsch A, Härdtle W (2007) The effects of windthrow on plant species richness in a Cenral European beech forest. Plant Ecol 191:47–65

Vuidot A, Paillet A, Archaux F, Gosselin F (2011) Influence of tree characteristics and forest management on tree microhabitats. Biol Conserv 144:441–450

Wells K, Böhm SM, Boch S, Fischer M, Kalko EKV (2011) Local and landscape-scale forest attributes differ in their impact on bird assemblages across years in forest production landscapes. Basic Appl Ecol 12:97–106

Wiedemann E (1951) Ertragskundliche und waldbauliche Grundlagen der Forstwirtschaft. JD Sauerländer‘s Verlag, Frankfurt am Main

Wilson KA, Underwood EC, Morrison SA, Klausmeyer KR, Murdoch WW et al (2007) Conserving biodiversity efficiently: what to do, where, and when. PLoS Biol 5(9):e223. doi:10.1371/journal.pbio.0050223

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. For Ecol Manag 255:1251–1261

Wubet T, Christ S, Schöning I, Boch S, Gawlich M, Schnabel B, Fischer M, Buscot F (2012) Differences in soil fungal communities between European beech (*Fagus sylvatica* L.) dominated Forests are related to soil and understory vegetation. PLoS ONE 7(10):e47500

Zhang Y, Chen HY, Reich PB (2012) Forest productivity increases with eveness, species richness and trait variation: a global metaanalysis. J Ecol. doi:10.1111/j.1365-2745.2011.01944.x

Zobel M, Pärtel M (2008) What determines the relationship between plant diversity and habitat productivity? Glob Ecol Biogeogr 17:679–684