

Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium

Margot Vanhellemont^{1,*}, Lander Baeten^{1,2} & Kris Verheyen¹

¹Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Gontrode, Belgium

²Terrestrial Ecology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat 35, BE-9000 Ghent, Belgium

*Author for correspondence: Margot.Vanhellemont@UGent.be

Background and aims – A renewed interest in the functional role and dynamics of forest understorey plant communities has led to an increasing number of publications that present the results of understorey resurveys. However, studies looking at the possible causes of temporal changes in the understorey often lack data on soil and tree layer conditions for the old survey. We investigated how changes in the tree layer, soil, and understorey were related in two contrasting forest types.

Methods – Full re-inventory of the tree layer (1997, 2010) and resurvey of the soil and understorey in 40 plots on a permanent grid (1993, 2011) in an ancient temperate deciduous forest. The 1.83 ha study area consisted of a part dominated by oak (*Quercus robur*) and beech (*Fagus sylvatica*) and a part dominated by ash (*Fraxinus excelsior*).

Key results – Overall, the basal area and shade-casting ability of the tree layer had increased. In the oak-beech forest, the soil pH had decreased; below ash, the topsoil pH had increased. The understorey species richness had increased, and the change in species richness was correlated with the change in soil pH and basal area, the latter in the oak-beech forest only. The observed patterns in understorey dissimilarity were different for the dataset including or excluding the regeneration of woody species.

Conclusions – The changes in soil and understorey differed between the two forest types, and there were some indications of recovery from soil acidification in the ash forest.

Key words – Permanent plots, resurvey, soil acidity, increased shade, herb layer, forest understorey, beta diversity partitioning, turnover, nestedness, multiple-site dissimilarity.

INTRODUCTION

Most of the plant species diversity of temperate forests is present in the understorey (Gilliam 2007). As the understorey also plays a significant role in the functioning of forests (Gilliam 2007), insight into changes in forest understoreys and the possible drivers of these changes is important for forest management and nature conservation. Temporal changes in the understorey of temperate deciduous forests have been attributed to atmospheric nitrogen deposition (e.g. Thimonier et al. 1992, 1994, Lameire et al. 2000, Bernhardt-Römermann et al. 2007), changes in forest management, canopy cover and composition (e.g. Van Calster et al. 2007, 2008, Baeten et al. 2009, Hédil et al. 2010, Verheyen et al. 2012), and changes in the abundance of large herbivores (e.g. Kirby & Thomas 2000, Rooney 2009, Royo et al. 2010).

The multiple environmental changes affecting forests concur, and they influence the understorey simultaneously, which makes it difficult to disentangle their relative contributions (see, e.g. Baeten et al. 2010a for a review of global

change impacts on *Anemone nemorosa*). Nitrogen accumulation, the main driver behind the impact of nitrogen deposition on plant species composition (Bobbink et al. 2010), has been found to reduce local understorey species richness and evenness, resulting in a loss of forest biodiversity (Gilliam 2006, Bobbink et al. 2010). Verheyen et al. (2012), however, found no directional change in species richness in their synthesis of 23 understorey resurveys in temperate forests in Europe, with increases just as likely as decreases. Compositional change, i.e. temporal turnover, was often strong and could not be explained by nitrogen deposition, but was mainly related to an increase in canopy cover and a higher share of tree species with easily decomposing leaf litter in the canopy (Verheyen et al. 2012). Canopy structure, cover, and species composition have been altered in many ancient, deciduous forests in lowland Europe due to the change in management from the historic coppice or coppice with standards to the present high forest (Van Calster 2008). Tree species affect the understorey differently through their species-specific shading ability (Canham et al. 1994) and litter quality (Van Oijen et al. 2005,

Koorem et al. 2011). Canopy cover affects the light availability at the forest floor and thus the species composition of the understorey (e.g. Vockenhuber et al. 2011). Sure enough, Kirby & Thomas (2000) did observe the largest declines in species richness in plots where the canopy cover had increased most, although grazing and browsing by deer were the main driver of understorey changes in their study.

Many forest understorey resurvey studies are based on semi-permanent plots (e.g. Van Calster et al. 2007, von Oheimb & Brunet 2007, Baeten et al. 2010b, Naaf & Wulf 2010, Jantsch et al. 2013). Due to a shift in plot location between the surveys in these studies, a part of the observed temporal turnover may actually quantify spatial turnover, the degree of which is generally unknown. Besides, resurvey studies exploring the possible causes of temporal understorey changes often have to rely on indirect measures of, e.g. soil conditions and light availability calculated based on the understorey composition itself, typically using the Ellenberg indicator values (e.g. Thimonier et al. 1992, 1994, Keith et al. 2009, Verstraeten et al. 2013b). The old survey may lack direct measurements of, for instance, soil (e.g. Thimonier et al. 1992, 1994, Lameire et al. 2000, Jantsch et al. 2013, Verstraeten et al. 2013b) or tree layer characteristics (e.g. Lameire et al. 2000, Cornelis et al. 2007). Furthermore, only a few resurvey studies have directly compared understorey

changes in contrasting forest types, e.g. Lameire et al. (2000) and Verstraeten et al. (2013b).

In this study, we resurveyed plots on a permanent grid in the intensively monitored area of an ancient forest, i.e. the Aelmoeseneie forest of Ghent University. As the forest in the study area has been developing spontaneously since 1995 and seeing the high level of nitrogen deposition at the site (e.g. Verstraeten et al. 2012a), we expected tree layer changes and soil acidification to be the main drivers of changes in species richness and composition of the forest's understorey. We analysed the temporal changes in the tree layer, soil, and understorey between 1993–1997 and 2010–2011, for two adjacent, currently unmanaged mixed deciduous stands dominated by either *Fraxinus excelsior* or *Fagus sylvatica* and *Quercus robur*.

MATERIALS AND METHODS

Study site

The Aelmoeseneie forest is a mixed deciduous forest of 28.5 ha at 11–21 m a.s.l. in northwestern Belgium (50°58'N 3°49'E; fig. 1). The soil developed from a quaternary layer of sandy loam on a shallow impermeable clay and sand complex of tertiary origin (FAO classification: Gleyic Cambisol). The mean annual temperature (1981–2010) at a nearby

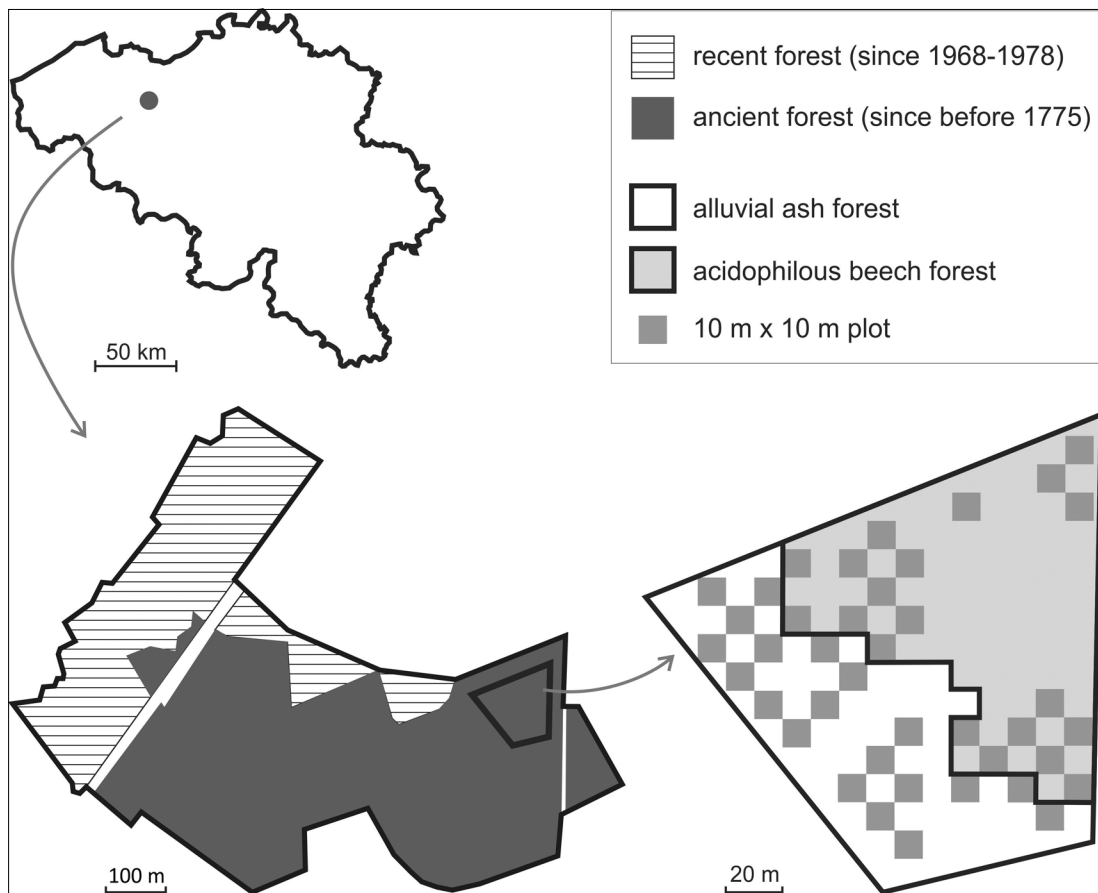


Figure 1 – Location of the Aelmoeseneie forest in Belgium; location of the study area in the ancient-forest part of the Aelmoeseneie forest; the two forest types and the 40 resurvey plots in the study area. As we focused on undisturbed plots, none of the grid plots inside the intensively monitored Level II plot, located on the right of the study area, were included in the resurvey.

Table 1 – Stem density (N) and basal area (BA) of the main tree and shrub species for the two forest types in the study area in 1997, 2005, and 2010.

The species with BA < 0.1 m² ha⁻¹ are included in the category ‘other’, i.e. *Alnus glutinosa* (L.) Gaertn., *Alnus incana* (L.) Moench, *Betula pubescens* Ehrh., *Crataegus monogyna* Jacq., *Ilex aquifolium* L., *Prunus avium* (L.) L., *Prunus serotina* Ehrh., and *Sorbus aucuparia* L.

species	alluvial ash forest						acidophilous beech forest					
	N (ha ⁻¹)			BA (m ² ha ⁻¹)			N (ha ⁻¹)			BA (m ² ha ⁻¹)		
	1997	2005	2010	1997	2005	2010	1997	2005	2010	1997	2005	2010
<i>Quercus robur</i> L.	37	33	33	2.81	3.13	3.41	146	129	122	13.77	15.21	15.81
<i>Fraxinus excelsior</i> L.	159	152	150	18.35	20.41	21.20	1	1	1	0.17	0.20	0.22
<i>Fagus sylvatica</i> L.	5	7	7	0.39	0.51	0.59	86	104	106	7.41	8.56	9.25
<i>Acer pseudoplatanus</i> L.	115	254	273	4.52	6.07	7.05	57	88	91	0.85	1.19	1.37
<i>Larix kaempferi</i> (Lambert) Carr.	7	7	7	1.31	1.43	1.51	19	19	19	3.48	3.77	3.95
<i>Quercus rubra</i> L.	1	1	1	0.01	0.02	0.02	4	5	4	0.78	1.02	1.06
<i>Populus alba</i> L.	9	7	4	1.92	2.01	1.05						
<i>Corylus avellana</i> L.	43	104	105	0.31	0.66	0.68	10	38	38	0.07	0.19	0.20
<i>Castanea sativa</i> Mill.	4	4	4	0.25	0.30	0.32	5	7	6	0.21	0.28	0.27
other	16	13	11	0.14	0.13	0.13	22	24	12	0.19	0.16	0.08
total	397	583	597	30.00	34.67	35.95	346	410	395	26.90	30.57	32.22

weather station was 10.6°C, and the mean annual precipitation was 786 mm, distributed equally over the year (Royal Meteorological Institute of Belgium). The southeastern part of the forest is ‘ancient’ forest, i.e. already marked as forest on the land-use maps of de Ferraris (1771–1778) and remained forested ever since (fig. 1). Almost the entire forest was cut during WWI and replanted in 1921–1922. For more details on the forest, see Vanhellemont & Verheyen (2011).

The 1.83 ha study area, located in the ancient forest part (fig. 1), consists of a 0.82 ha zone with ash (*Fraxinus excelsior*) close to a small brook and a more elevated 1.01 ha zone with oak (*Quercus robur*) and beech (*Fagus sylvatica*) (table 1). The two zones of the study area can be classified as the Natura 2000 habitat types ‘alluvial forest with *Alnus glutinosa* and *Fraxinus excelsior*’ (code 91E0) and ‘Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrublayer’ (code 9120). Further on, we will refer to the two forest types as ‘(alluvial) ash forest’ and ‘(acidophilous) beech forest’. The study area was fenced in 1993 and has not been managed since 1995. In the study area, the condition of the forest has been intensively monitored in a Level II observation plot of the international co-operative programme on the assessment and monitoring of air pollution effects on forests (<http://icp-forests.net>) since 1988 (e.g. Verstraeten et al. 2012a).

Nomenclature

Nomenclature follows Lambinon et al. (1998).

Data collection

Tree layer data were collected in the entire study area. A full inventory of all trees and shrubs with a diameter at breast height > 7 cm was performed after the growing seasons of 1997 (December 1997), 2005 (January 2006), and 2010 (September 2010) (Vande Walle 2007, De Couck 2011). The

position (x,y coordinates), species, circumference (cm), and status (dead or alive) of each tree were noted.

Data on the understorey, forest floor, and soil were collected in plots of 100 m² located on a 10 × 10 m grid. In 1993, 71 plots were fully investigated. In 2010/2011, we resurveyed only the plots that appeared undisturbed. We excluded the plots crossed by the path through the study area, plots inside the level II plot (fig. 1), and plots that had been disturbed by recent research projects (e.g. Staelens et al. 2008, De Frenne et al. 2010). In the end, we included 40 of the 71 plots in our resurvey: 20 plots in the ash forest zone and 20 plots in the beech forest zone (fig. 1). During the understorey surveys in the spring of 1993 and in April 2011, the cover of all herbaceous and woody plant species smaller than 2 m was estimated in the 100 m² plots (Sterken 1993). The forest floor was sampled in a 0.5 × 0.5 m square in the plot centre in spring 1993 or at 1 m distance from the plot centre in October 2010, just before leaf fall (Haleplis & Vakalopoulos 1993, De Couck 2011). The necromass of the litter, fragmentation, and humus layer was determined separately. After the removal of the forest floor, soil cores were taken in the four corners of the 0.5 × 0.5 m sampling square. For each plot, a mixed soil sample for the soil layers of 0–5 cm and 5–15 cm depth was collected. The soil samples were dried, ground, and their pH KCl was measured with a glass electrode (Orion, model 920A) after extracting 14 ml soil in a 70 ml KCl (1 M) solution.

Data analysis

To investigate temporal changes in the tree layer, soil, and understorey for the two forest types in the study area, we first derived several variables from the forest inventory and resurvey data to characterize the tree layer and understorey. The forest floor necromass data were only used to characterize the two forest types and not for the analysis of temporal changes, seeing the difference in collection date, i.e. spring

1993 vs. early autumn 2010. Calculations and analysis were done with R version 3.0.1 (R Core Team 2013); graphs were made with the R package *ggplot2* (Wickham 2009).

Tree layer characteristics – For each tree and shrub species i in the full inventories of 1997, 2005, and 2010, we calculated basal area (BA_i , $\text{m}^2 \text{ha}^{-1}$), stem density (N_i , ha^{-1}), and the importance value, i.e. the mean of the relative basal area and the relative density: $1/2 (BA_i / BA_{type} + N_i / N_{type})$ (Parker et al. 1985). The calculations were done separately for the two forest types in the study area. For each of the 10×10 m plots, we calculated the plot's basal area ($\text{m}^2 \text{ha}^{-1}$) for 1997 and 2010, based on all the trees and shrubs growing in the plot or within a buffer of 1 m around the plot. We then calculated the shade-casting ability (SCA) and litter quality (LQ) of the tree layer, weighted by basal area, for each plot (cf. Van Calster et al. 2007, 2008, Baeten et al. 2009, Verheyen et al. 2012). The ordinal indices SCA and LQ describe the shade-casting ability, from 1 (low) to 6 (high), and litter quality, from 1 (slow) to 5 (fast litter decomposition), of tree and shrub species (see electronic appendix 1).

Understorey characterization – The vegetation data were converted to presence/absence data. We looked at the entire understorey, i.e. herbaceous and woody species, as well as at the herbaceous species only to investigate whether including woody species regeneration affects the observed understorey diversity patterns. We first calculated each plot's species richness, i.e. the number of species or alpha diversity, for 1993 and 2011. For each forest type and each year, we then calculated beta diversity using the multiple-site dissimilarity measures proposed by Baselga (2010) with the R package *betapart* (Baselga & Orme 2012, Baselga et al. 2013). Baselga (2013) demonstrated that the mean of the pairwise dissimilarities for all the plots within a site may not accurately reflect the site's overall heterogeneity in species composition because a pairwise dissimilarity, by definition, cannot account for, e.g. species co-occurrences among more than two plots. Beta diversity, i.e. the variation in species composition among plots, can be the result of real species replacement between plots, creating turnover patterns, and species loss or gain from plot to plot, creating a nestedness pattern. Thus, the turnover component of beta diversity accounts for the dissimilarity between plots that is caused by the substitution of some species in one plot by other species in another plot. The nestedness component accounts for the differences in composition between plots if no species is replaced from one plot to the other; the species composition of the plot with the lowest species richness is a subset of the plot with the higher species richness (see Baselga (2010) and Baeten et al. (2012, in press) for some hypothetical examples). We quantified beta diversity using an additive partitioning of the overall compositional dissimilarity, expressed by the multiple-site analogue of the Sørensen dissimilarity index (β_{SOR}), into a turnover term, i.e. the Simpson dissimilarity index (β_{SIM}), and a nestedness-resultant dissimilarity term (β_{SNE}) (Baselga 2010). Investigating the turnover and nestedness components of beta diversity separately can be useful for understanding biodiversity patterns across multiple sites (e.g. Baselga 2010, Baeten et al. 2012).

Temporal changes – To determine the changes in the tree layer variables, soil pH, and understorey species richness for the two forest types, we calculated the response ratio for each variable as the natural logarithm of the proportional change in its mean value for the new and the old survey, i.e.

$\ln(\bar{X}_{\text{new}} / \bar{X}_{\text{old}})$. As these means are based on repeated measurements in the same plots, we calculated the 95% confidence intervals around the response ratio accounting for the covariance between the measurements of the two surveys (Lajeunesse 2011).

We calculated the temporal turnover in plot-level community composition between 1993 and 2011 using beta diversity metrics and the additive partitioning of Baselga (2010). Since we compared only two communities, i.e. the same plot in the two surveys, we calculated pairwise dissimilarities (β_{SOR} , β_{SIM} , β_{SNE}) instead of their multiple-site analogues using the R package *betapart* (Baselga & Orme 2012, Baselga et al. 2013). For each forest type, we then calculated the mean of the pairwise dissimilarities for the plots in the forest type. Baeten et al. (2012) clearly showed that the partitioning of beta diversity can reveal patterns of compositional homogenization that are masked in a standard beta diversity analysis. In their study, overall beta diversity remained similar over time, but the variation in species composition among plots shifted towards a situation with reduced true species turnover between plots and increased nestedness, i.e. plots with few species became, to a larger extent, subsets of species-rich plots. To test the significance of the changes in the compositional heterogeneity of a forest type between the two surveys of our study, we used a resampling procedure, taking 100 random samples of 15 plots and computing the mean and standard deviation of the resulting distribution of the multiple-site beta measures (cf. Baselga & Orme 2012).

We investigated the species-level patterns of change in the understorey following the approach of Baeten et al. (in press). Using species-level binomial models, we tested for each species whether its frequency was significantly different in 1993 and 2011, for each of the two forest types. Species that decrease their heterogeneity of occurrence, i.e. rare species that become more rare or prevalent species that become more prevalent, will cause the plots to become more homogeneous in composition. The loss of rare species, for instance, causes lower compositional variation in the sense that most plots will lack those species. Baeten et al. (in press) refer to these species as 'community-convergence species' as opposed to the 'community-divergence species' that increase community heterogeneity.

We then looked for correlations between the changes in plot-level understorey richness and temporal turnover in beta diversity on the one hand and the changes in the tree layer and soil characteristics on the other hand. To analyse the relationship between changes in diversity and the significantly correlated variables, we performed multiple linear regressions with the *gls* function of the *nlme* library (Pinheiro et al. 2013). Adding a spatial correlation structure did not result in significantly better models.

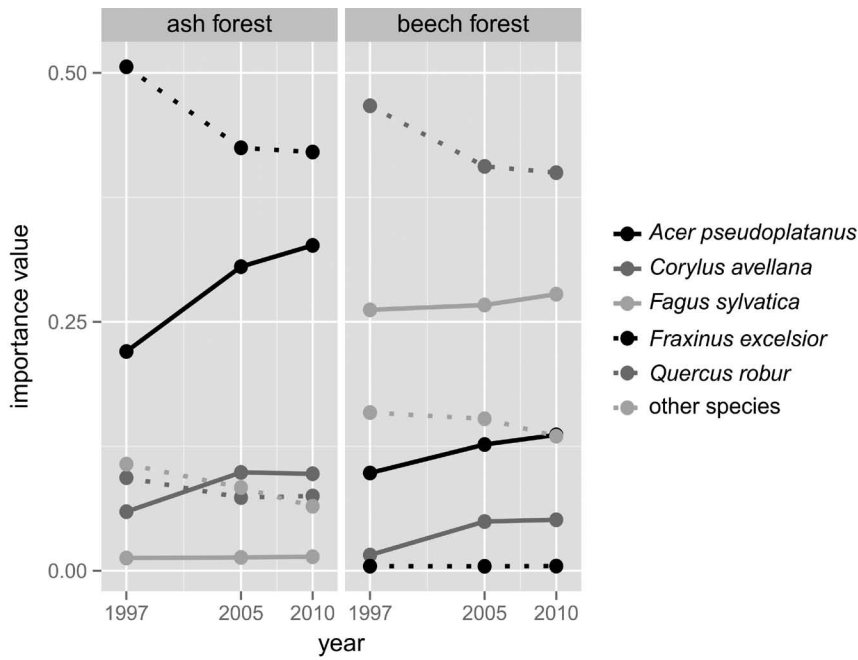


Figure 2 – Changes in the importance value of tree species for the two forest types in the study area between 1997 and 2010. The category ‘other species’ contains the tree and shrub species that showed no clear changes in importance value. Solid lines represent shade-tolerant species; dotted lines represent light-demanding species.

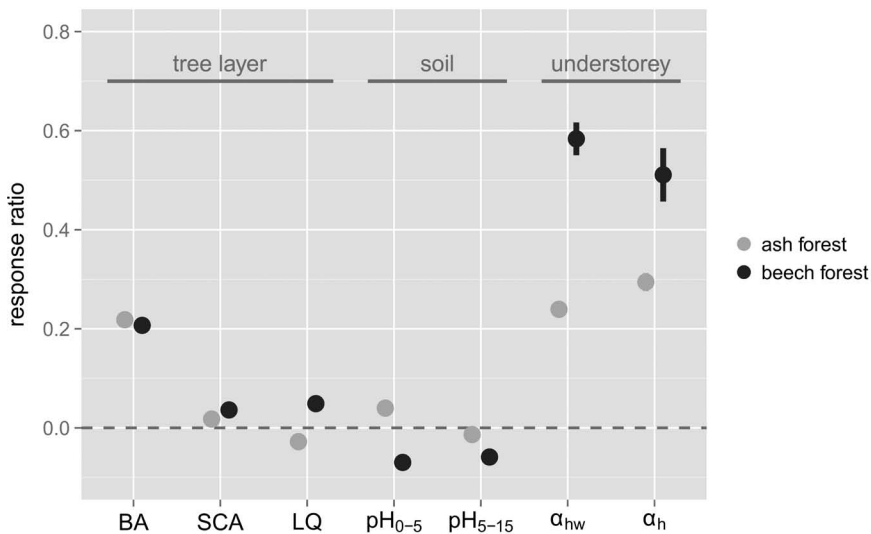


Figure 3 – Changes in the tree layer (1997–2010), soil (1993–2010), and understorey (1993–2011) for the two forest types in the study area. Response ratio, i.e. the natural logarithm of the ratio of the means for the new and old survey, with 95% confidence interval for the tree layer variables - basal area (BA), shade-casting ability (SCA), and litter quality (LQ); the soil variables - pH KCl topsoil layer, i.e. 0–5 cm (pH₀₋₅), and soil layer at 5–15 cm depth (pH₅₋₁₅); the understorey variables - number of herbaceous as well as woody species (α_{hw}) and number of herbaceous species only (α_h)

RESULTS

The two forest types in the study area showed clear differences in forest floor necromass, soil pH and understorey species richness (electronic appendix 2). In the ash forest, the shade-casting ability and litter quality of the tree layer were higher, the pH of both soil layers was higher (only marginally significantly so for the 5–15 cm soil layer in 1993), and

the number of understorey species per plot was larger. The necromass of the forest floor was larger in the beech forest.

The basal area increased in both forest types over the 13-year monitoring period. The increase in stem density, most explicit in the ash forest, occurred mainly between 1997 and 2005. Most of the ingrowth were shade-tolerant species such as *Acer pseudoplatanus*, *Fagus sylvatica*, and *Corylus avellana* (table 1). Mortality was highest for the light-demanding species, i.e. *Quercus robur*, mainly in the beech forest

Table 2 – Overall species richness (γ) and mean species richness per plot (α) for the two forest types in the study area in 1993 and 2011.

Values are shown for the entire understorey, i.e. herbaceous as well as woody species, and for the herbaceous species only. Standard deviations are given between brackets. P values represent the significance of the difference in species richness between both years (Wilcoxon signed-rank test).

forest type	γ		α		p
	1993	2011	1993	2011	
	<i>herbaceous + woody</i>				
alluvial ash	35	44	13.5 (4.3)	17.2 (4.9)	< 0.001
acidophilous beech	16	26	5.3 (1.8)	9.5 (3.1)	< 0.001
	<i>herbaceous</i>				
alluvial ash	26	30	9.4 (4.0)	12.6 (4.7)	< 0.001
acidophilous beech	9	14	2.6 (1.2)	4.3 (2.4)	0.003

(table 1). The importance values also showed an increase in importance of shade-tolerant species and a decrease of light-demanding species (fig. 2). The increase in shade-casting ability was larger in the beech forest than in the ash forest (fig. 3).

The litter quality index of the tree layer increased in the beech forest (fig. 3) because of changes in the proportion of species with slowly-decomposing litter (*Quercus*, *Fagus*) and faster-decomposing litter (*Acer*, *Corylus*) in the overall basal area. In the ash forest, the litter quality indices of the plots decreased (fig. 3) due to a decrease in the contribution of *Fraxinus* to the overall plot basal area. The opposite changes in the tree layer litter quality index for the two forest types mirrored the changes in soil pH (fig. 3). In the ash forest, the pH of the topsoil layer increased between 1993 (mean pH = 3.39) and 2010 (3.53), and the pH of the soil at 5–15 cm depth dropped only a little (3.43 to 3.38). In the beech forest, the pH decreased in both soil layers (0–5 cm: 3.19 to 2.98, 5–15 cm: 3.33 to 3.14).

The species richness of the understorey increased considerably in both forest types between 1993 and 2011 (table 2, fig. 3). The species pool and mean species richness per plot were larger in the ash forest (table 2), but the relative increase in species richness was larger in the beech forest (fig. 3). Ten species were new in the 2011 survey, i.e. in decreasing order of frequency (see appendix 3), *Quercus robur*, *Castanea sativa*, *Ilex aquifolium*, *Carex sylvatica*, *Crataegus monogyna*, *Luzula pilosa*, *Athyrium filix-femina*, *Quercus rubra*, and *Stachys sylvatica*. Only three species, with a low frequency in 1993, were no longer present in 2011, i.e. *Cardamine flexuosa*, *Rumex obtusifolius*, and *Maianthemum bifolium*. Mainly woody species showed a significant increase in frequency between the two surveys, in the beech forest in particular (fig. 4, electronic appendix 3). In addition, the prevalence of *Dryopteris* spp. significantly increased in the two forest types; *Arum maculatum* and *Geum urbanum* increased in the ash forest; and *Hedera helix* increased in the beech forest. *Fraxinus excelsior* was the only species that

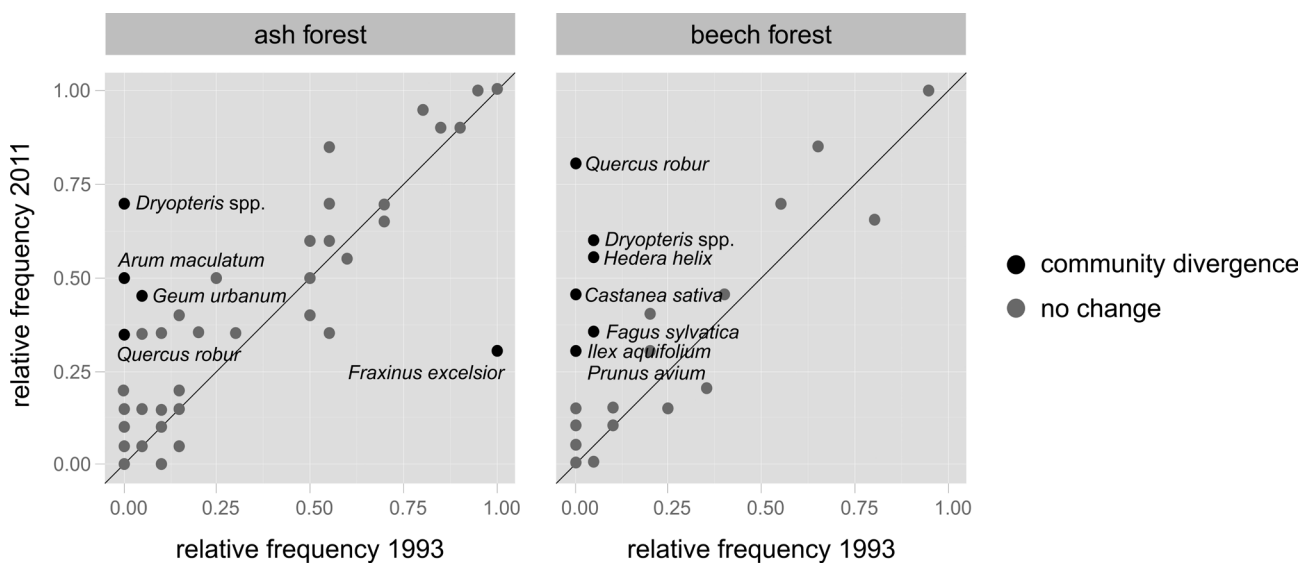


Figure 4 – The changes in relative frequency of the understorey species between 1993 and 2011 for the two forest types in the study area. The species whose frequency did not change significantly are scattered around the 1:1 line of no change. The species names are given for the community-divergence species, the species that showed a significant change in frequency. Except for *Fraxinus excelsior*, these species were relatively rare (or absent) in 1993 and increased between the two surveys.

Table 3 – Linear regression models of the change in understorey species richness.

Changes in understorey species richness are modelled in function of the changes in topsoil pH (ΔpH_{0-5}) and basal area (ΔBA), and the forest type in the study area (ash vs. beech). The parameter values, their standard error (SE), and p value (p) are reported for the models with the largest goodness of fit, for the entire understorey, i.e. herbaceous as well as woody species, and for the herbaceous species only.

variable	herbaceous + woody			herbaceous		
	value	SE	p	value	SE	p
intercept	2.20	1.37	0.115	2.14	1.06	0.050
ΔpH_{0-5}	4.82	1.81	0.012	4.23	1.40	0.005
ΔBA	7.28	11.04	0.514	4.42	8.53	0.607
forest type	5.00	1.84	0.010	2.24	1.42	0.123
$\Delta \text{BA} : \text{forest type}$	-30.74	14.51	0.041	-25.57	11.21	0.029
R^2_{adj}		0.19			0.34	
p		0.02			< 0.001	

Table 4 – Temporal turnover (1993–2011) of the understorey for the two forest types in the study area.

Mean of the pairwise dissimilarity between the old and new survey (β_{sor}) and its turnover (β_{sim}) and nestedness components (β_{sne}) for each plot; standard deviation between brackets. Values are shown for the entire understorey, i.e. herbaceous as well as woody species, and for the herbaceous species only.

forest type	$\bar{\beta}_{\text{sor}}$	$\bar{\beta}_{\text{sim}}$	$\bar{\beta}_{\text{sne}}$
	<i>herbaceous + woody</i>		
alluvial ash	0.291 (0.109)	0.186 (0.123)	0.105 (0.062)
acidophilous beech	0.446 (0.118)	0.224 (0.125)	0.222 (0.140)
	<i>herbaceous</i>		
alluvial ash	0.262 (0.127)	0.124 (0.132)	0.139 (0.094)
acidophilous beech	0.442 (0.252)	0.200 (0.335)	0.242 (0.173)

showed a significant decrease in frequency. The changes in species richness were positively correlated with the change in the topsoil pH and negatively correlated – in the beech forest – with the change in basal area (table 3).

For the herbaceous species, in c. half of the plots, there was no species replacement ($\beta_{\text{sim}} = 0$), only species loss or gain ($\beta_{\text{sne}} > 0$) between the two inventories (results not shown). For the entire understorey in the ash forest, species replacement (β_{sim}) contributed more to the overall temporal turnover than species loss or gain (β_{sne} , table 4). We found no significant correlations between the temporal turnover in beta diversity and any of the tree layer or soil characteristics. In both survey years, the multiple-site dissimilarity (β_{SOR} , fig. 5) mostly resulted from species replacement between plots (spatial turnover, β_{SIM}). The overall heterogeneity in the pool of plots was larger (mean \pm sd for 2011, herbs = h, herbs+woody = hw) in the beech forest ($\beta_{\text{SOR-h}}$: 0.810 ± 0.011 ; $\beta_{\text{SOR-hw}}$: 0.788 ± 0.007) than in the ash forest ($\beta_{\text{SOR-h}}$: 0.754 ± 0.011 ; $\beta_{\text{SOR-hw}}$: 0.773 ± 0.010). Looking at the entire understorey, the multiple-site dissimilarity measures showed no changes between the surveys in the beech forest, but in the ash forest, the nestedness component (β_{SNE}) contributed more to the overall beta diversity in 1993 than in 2011 (fig. 5). Looking at the herbaceous species only, clear changes were only apparent for the beech forest: β_{SNE} contributed more to the overall heterogeneity in herbaceous species composition in 2011 than in 1993 (fig. 5).

DISCUSSION

The study area was fenced in 1993 and has not been managed since 1995. Thus, the study period (1993–2011) represents a period of rather undisturbed forest development. The observed increase in basal area and the ingrowth of shade-casting, late-successional species such as *Acer pseudoplatanus* and *Fagus sylvatica* match the observations in many studies in temperate deciduous forests in Europe (see Verheyen et al. 2012). The general increase in litter quality over time observed by Verheyen et al. (2012) was only apparent in the beech forest in our study. Yet, the forest floor necromass in the beech forest remained much higher than in the ash forest. De Schrijver et al. (2012) also saw no buildup of forest floor necromass under *Fraxinus excelsior* vs. a clear forest floor buildup under *Quercus robur* after 35 years of post-agricultural forest development. The accumulation of slowly decomposing litter in a forest floor will lead to soil acidification (Nilsson et al. 1982), and, indeed, the soil became more acid in the beech forest part of our study area, similar to the findings of other resurvey studies in temperate forests (e.g. Van Calster et al. 2007, Baeten et al. 2009).

Litter accumulation and soil acidification are natural consequences of tree growth and forest maturation (Nilsson et al. 1982), but nitrogen accumulation due to atmospheric nitrogen deposition can reinforce both processes (Bobbink et al. 2010). Yet, the tree species can influence the degree to which nitrogen deposition induces soil acidification (De Schrijver et al. 2012). De Schrijver et al. (2012), for instance,

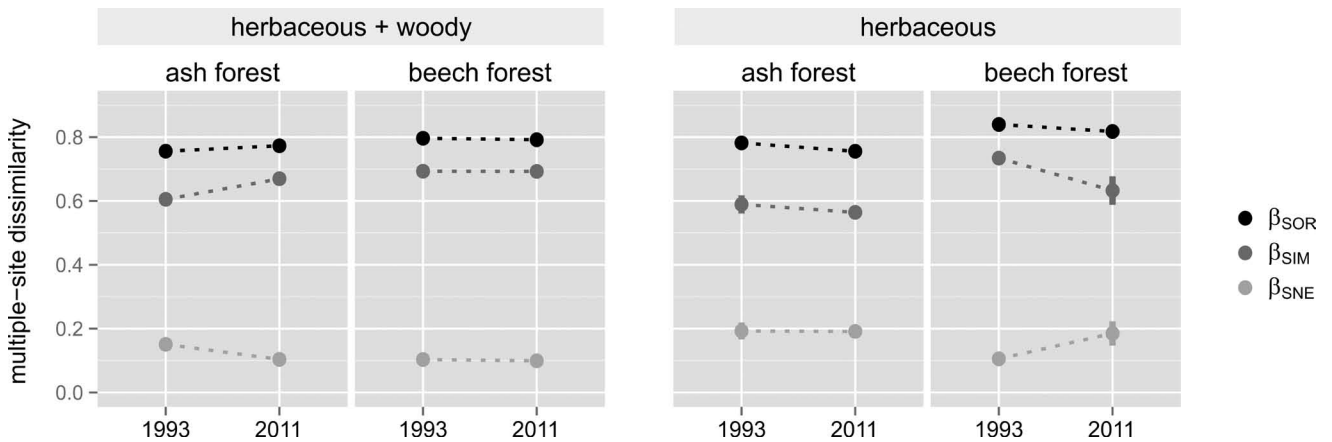


Figure 5 – Overall heterogeneity in the understorey of the plots (β_{SOR}) and its turnover (β_{SIM}) and nestedness components (β_{SNE}) for the two forest types in the study area in 1993 and 2011. Mean and standard deviation of the multiple-site dissimilarity values based on resampling ($n = 100$) of the plots ($n = 15$) in each forest type. Values are shown for the entire understorey, i.e. herbaceous as well as woody species, and for the herbaceous species only.

found a much lower topsoil pH below *Quercus robur* than below *Fraxinus excelsior* after 35 years of forest development in stands receiving similar nitrogen deposition levels. In our study, the topsoil pH below ash even increased over time. This increase in soil pH probably indicates a first step towards recovery from acidification following the decrease in atmospheric deposition at the study site (see next paragraph). Similarly, Vangelova et al. (2010) and Akselsson et al. (2013) also saw an increase in soil solution pH, but at 50 cm depth, in some of the forests they investigated in the UK and southern Sweden. As a result of the increase in soil pH, 13 out of the 20 plots in the ash zone appeared to be in the cation exchange buffer range, i.e. pH H_2O of the soil > 4.2 (*sensu* Ulrich 1991), in 2010, as opposed to 7 out of 20 in 1993. All the plots in the beech forest were in the aluminium buffer range, i.e. with pH $H_2O < 4.2$. The mean pH H_2O values in 2010 were 4.5 (0–5 cm) and 4.3 (5–15 cm) in the ash forest and 3.8 (0–5 cm) and 3.9 (5–15 cm) in the beech forest. The 4.2 pH threshold is considered critical for the successful establishment and growth of herbaceous understorey species of deciduous forests (Falkengren-Grerup & Tyler 1993). Acid-intolerant species such as *Arum maculatum* and *Primula elatior* (cf. Thomaes et al. 2012), present in the ash forest of the study area, will most likely benefit from the recovery of soil acidification.

Bulk nitrogen deposition, measured close to the study area, decreased between 1993 and 2011, i.e. from 25.0 to 10.0 kg ha⁻¹ yr⁻¹. Similarly, the stand nitrogen deposition in the level II plot in the study area decreased, from 33.7 kg ha⁻¹ yr⁻¹ in 1993 to 15.0 kg ha⁻¹ yr⁻¹ in 2011 (A. Verstraeten, pers. comm.). Notwithstanding the decrease, the nitrogen deposition in the study area was still high and within the range of the critical loads reported by Bobbink et al. (2010), who stated that nitrogen deposition can cause loss of understorey species diversity and alter the species composition of forest understoreys if the deposition exceeds 20, or even 10–15, kg ha⁻¹ yr⁻¹. Yet, we did see an overall increase in species richness between the old and new survey. Other resurvey studies have found increases as well as decreases in species rich-

ness. Of the 23 studies included in Verheyen et al. (2012), for instance, 9 showed an increase and 8 a decrease in species richness. In our study, the increase in species richness was largest in plots in which the soil pH increased most, and, below beech, in the plots with the smallest increase in basal area. Baeten et al. (2009) also identified changes in basal area and soil acidity as the main driving forces for changes in herb layer composition, and Kirby & Thomas (2000) also found a clear correlation between the change in understorey species number and the change in tree layer cover.

Understorey resurvey studies have included (e.g. Verheyen et al. 2012, Jantsch et al. 2013, Verstraeten et al. 2013a, 2013b) or excluded (e.g. Kirby & Thomas 2000, Van Calster et al. 2008, Baeten et al. 2009, Naaf & Wulf 2010) the regeneration of tree and shrub species in their analysis of temporal change. For instance, Van Calster et al. (2008) and Baeten et al. (2009) excluded the woody seedlings to keep irregular mast events from clouding long-term trends in the vegetation composition. Yet, mast years might become more frequent under global change (see, e.g. Övergaard et al. 2007 for beech in Sweden), which may result in woody seedlings being present more frequently. In the study area, good seed years or mast years for oak and beech occurred each 2–3 years between 1999 and 2011 (Verstraeten et al. 2012b). Similar to our observations, many resurvey studies did find an increase in woody species presence (e.g. Thimonier et al. 1992, Verheyen et al. 2012, Jantsch et al. 2013).

Excluding vs. including the woody species in our understorey dataset lead to differing results. For instance, the temporal turnover in beta diversity for the herbaceous species was the result of species losses or gains between the old and new survey for many plots, similar to the findings of Kirby & Thomas (2000). Plots lost or gained, mainly gained, herbaceous species over time. When looking at the herbaceous + woody species, the temporal turnover of almost all plots was the result of species losses or gains as well as species replacement. These contrasting findings suggest that the presence of a certain woody species in the understorey can be ephemeral. Capturing the seedling dynamics in a forest

understorey will thus require more frequent vegetation surveys. The multiple-site dissimilarity measures also tell a different story for the two datasets. Looking at the herbaceous species only, the overall heterogeneity decreased in both forest types, and the species composition pattern of the plots became more nested in the beech forest, i.e. plots were to a larger extent subsets of each other in 2011 (β_{NES} 0.104 \pm 0.017 in 1993, 0.191 \pm 0.040 in 2011). In the beech forest, no changes were observed for the herbaceous + woody species. By contrast, in the ash forest, there was a clear decrease in the nestedness measure (β_{NES}), a clear increase in the species replacement measure (β_{SIM}), and a slight increase in the overall diversity measure (β_{SOR}) for the herbaceous + woody species. Thus, the heterogeneity of the plots in the ash forest became larger, looking at the entire understorey, because of a higher amount of true species turnover between plots. The higher heterogeneity among plots in the ash forest in the recent survey was probably caused by the beginning of gap dynamics in this part of the study area, resulting from the formation of the first canopy gaps through windfall or die-back of canopy trees.

Our resurvey spanned a relatively short time period and compared only two moments in time, yet yielded some remarkable results. Seeing the permanent nature of the plots, long-term repeated monitoring is certainly feasible, and it will be highly interesting to examine whether the observed changes will be confirmed over time. Verheyen et al. (2012) and Baeten et al. (in press), for instance, found that the time interval between surveys is related to the degree of change in understorey species richness and composition. Besides, the gradual transition to an old growth stage characterized by the emergence of canopy gaps - the onset of which is already apparent in the ash forest - will initiate new understorey dynamics in the study area. The continuous monitoring of the atmospheric nitrogen deposition in the Level II plot in the study area represents an extra asset for the monitoring of future understorey changes and makes the study area most suitable to monitor the trajectory of ecosystem recovery after a period of very high atmospheric deposition. The different forest ecosystem components will probably change in different ways and at different rates.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of: (1) litter quality and shade-casting ability indices used for calculating the litter quality and shade-casting ability of the tree layer; (2) comparison of the tree layer, forest floor, soil, and understorey characteristics for the two forest types in the study area in the old and recent survey; and (3) frequency of the understorey species in the 10 \times 10 m plots for the two forest types in the study area in 1993 and 2011.

ACKNOWLEDGEMENTS

We thank Nathasja De Couck for her help with the 2010 data collection, Luc Willems and Greet De Bruyn for the laboratory work, and an anonymous reviewer for his valuable com-

ments on the manuscript. This paper was written while MV held a postdoctoral fellowship of the Special Research Fund (BOF) of Ghent University and LB was funded as postdoctoral fellow of FWO-Vlaanderen.

REFERENCES

- Akselsson C., Hultberg H., Karlsson P.E., Karlsson G.P., Hellsten S. (2013) Acidification trends in south Swedish forest soils 1986–2008 – Slow recovery and high sensitivity to sea-salt episodes. *Science of the Total Environment* 444: 271–287. <http://dx.doi.org/10.1016/j.scitotenv.2012.11.106>
- Baeten L., Bauwens B., De Schrijver A., De Keersmaecker L., Van Calster H., Vandekerckhove K., Roelandt B., Beeckman H., Verheyen K. (2009) Herb layer changes (1954–2000) related to the conversion of coppice-with standards forest and soil acidification. *Applied Vegetation Science* 12: 187–197. <http://dx.doi.org/10.1111/j.1654-109X.2009.01013.x>
- Baeten L., De Frenne P., Verheyen K., Graae B.J., Hermy M. (2010a) Forest herbs in the face of global change: a single-species-multiple-threats approach for *Anemone nemorosa*. *Plant Ecology and Evolution* 143: 19–30. <http://dx.doi.org/10.5091/plecevo.2010.414>
- Baeten L., Hermy M., Van Daele S., Verheyen K. (2010b) Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology* 98: 1447–1453. <http://dx.doi.org/10.1111/j.1365-2745.2010.01711.x>
- Baeten L., Vangansbeke P., Hermy M., Peterken G., Vanhuyse K., Verheyen K. (2012) Distinguishing between turnover and nestedness in the quantification of biotic homogenization. *Biodiversity and Conservation* 21: 1399–1409. <http://dx.doi.org/10.1007/s10531-012-0251-0>
- Baeten L., Warton D.I., Van Calster H., De Frenne P., Verstraeten G., Bonte D., Bernhardt-Römermann M., Cornelis J., Decocq G., Eriksson O., Hédli R., Heinken T., Hermy M., Hommel P., Kirby K., Naaf T., Petřík P., Walther G.-R., Wulf M., Verheyen K. (in press) A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution*. <http://dx.doi.org/10.1111/2041-210X.12137>
- Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134–143. <http://dx.doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga A. (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography* 36: 124–128. <http://dx.doi.org/10.1111/2041-210X.12029>
- Baselga A., Orme C.D.L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3: 808–812. <http://dx.doi.org/10.1111/j.2041-210X.2012.00224.x>
- Baselga A., Orme D., Villeger S. (2013) betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.2. Available from <http://CRAN.R-project.org/package=betapart> [accessed 13 Dec. 2013]
- Bernhardt-Römermann M., Kudernatsch T., Pfadenhauer J., Kirchner M., Jakobi G., Fischer A. (2007) Long-term effects of nitrogen deposition on vegetation in a deciduous forest near Munich, Germany. *Applied Vegetation Science* 10: 399–406. <http://dx.doi.org/10.1111/j.1654-109X.2007.tb00439.x>
- Bobbink R., Hicks K., Galloway J., Spranger T., Alkemade R., Ashmore M., Bustamante M., Cinderby S., Davidson E., Dentener F., Emmett B., Erismann J.-W., Fenn M., Gilliam F., Nordin A., Pardo L., De Vries W. (2010) Global assessment of nitrogen

- deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20: 30–59. <http://dx.doi.org/10.1890/08-1140.1>
- Canham C.D., Finzi A.C., Pacala S.W., Burbank D.H. (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24: 337–349. <http://dx.doi.org/10.1139/x94-046>
- Cornelis J., Rombouts L., Hermy M. (2007) Veranderingen in de vegetatie van de Herenbossen in Hulshout sinds 1980. Zijn effecten van verdroging, verzuring en vermessing merkbaar? *Natuur.focus* 6: 4–10.
- De Couck N. (2011) Veranderingen in de boomlaag in het Aelmoeseeneibos en de impact op strooisel, bodem en kruidlaag. MSc thesis, Ghent University, Ghent, Belgium.
- De Frenne P., De Schrijver A., Graae B.J., Gruwez R., Tack W., Vandeloek F., Hermy M., Verheyen K. (2010) The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. *Ecological Research* 25: 163–171. <http://dx.doi.org/10.1007/s11284-009-0640-3>
- De Schrijver A., De Frenne P., Staelens J., Verstraeten G., Muys B., Vesterdal L., Wuyts K., Van Nevel L., Schelfhout S., De Neve S., Verheyen K. (2012) Tree species traits cause divergence in soil acidification during four decades of postagricultural forest development. *Global Change Biology* 18: 1127–1140. <http://dx.doi.org/10.1111/j.1365-2486.2011.02572.x>
- Falkengren-Grerup U., Tyler G. (1993) Experimental evidence for the relative sensitivity of deciduous forest plants to high soil acidity. *Forest Ecology and Management* 60: 311–326. [http://dx.doi.org/10.1016/0378-1127\(93\)90086-3](http://dx.doi.org/10.1016/0378-1127(93)90086-3)
- Gilliam F.S. (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology* 94: 1176–1191. <http://dx.doi.org/10.1111/j.1365-2745.2006.01155.x>
- Gilliam F.S. (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845–858. <http://dx.doi.org/10.1641/B571007>
- Haleplis K.D., Vakalopoulos V.S. (1993) Carbon accumulation and pH variation in a mixed hardwood stand. Ma thesis, Ghent University, Ghent, Belgium & Aristotelian University of Thessaloniki, Thessaloniki, Greece.
- Hédli R., Kopecký M., Komárek J. (2010) Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity and Distributions* 16: 267–276. <http://dx.doi.org/10.1111/j.1472-4642.2010.00637.x>
- Jantsch M.C., Fischer A., Fischer H.S., Winter S. (2013) Shift in plant species composition reveals environmental changes during the last decades: a long-term study in beech (*Fagus sylvatica*) forests in Bavaria, Germany. *Folia Geobotanica* 48: 467–491. <http://dx.doi.org/10.1007/s12224-012-9148-7>
- Keith S., Newton A., Morecroft M.D., Bealey C.E., Bullock J.M. (2009) Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society B Biological Sciences* 276: 3539–3544. <http://dx.doi.org/10.1098/rspb.2009.0938>
- Kirby K.J., Thomas R.C. (2000) Changes in the ground flora in Wytham Woods, southern England from 1974 to 1991 – implications for nature conservation. *Journal of Vegetation Science* 11: 871–880. <http://dx.doi.org/10.2307/3236557>
- Koorem K., Price J.N., Moora M. (2011) Species-specific effects of woody litter on seedling emergence and growth of herbaceous plants. *PLoS ONE* 6(10): e26505. <http://dx.doi.org/10.1371/journal.pone.0026505>
- Lajeunesse M.J. (2011) On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology* 92: 2049–2055. <http://dx.doi.org/10.1890/11-0423.1>
- Lambinon J., De Lange J.E., Delvosalle L., Duvigneaud J. (1998) Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. Meise, Nationale Plantentuin van België.
- Lameire S., Hermy M., Honnay O. (2000) Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. *Journal of Vegetation Science* 11: 695–704. <http://dx.doi.org/10.2307/3236576>
- Naaf T., Wulf M. (2010) Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biological Conservation* 143: 848–855. <http://dx.doi.org/10.1016/j.biocon.2009.12.027>
- Nilsson S.I., Miller H.G., Miller J.D. (1982) Forest growth as a possible cause of soil and water acidification: an examination of the concepts. *Oikos* 39: 40–49. <http://dx.doi.org/10.2307/3544529>
- Övergaard R., Gemmel P., Karlsson M. (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* 80: 555–565. <http://dx.doi.org/10.1093/forestry/cpm020>
- Parker G.R., Leopold D.J., Eichenberger J.K. (1985) Tree dynamics in an oldgrowth, deciduous forest. *Forest Ecology and Management* 11: 31–57. [http://dx.doi.org/10.1016/0378-1127\(85\)90057-X](http://dx.doi.org/10.1016/0378-1127(85)90057-X)
- Pinheiro J., Bates D., DebRoy S., Sarkar D., R Development Core Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-109.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/> [accessed 13 Dec. 2013].
- Rooney T.P. (2009) High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology* 202: 103–111. <http://dx.doi.org/10.1007/s11258-008-9489-8>
- Royo A.A., Collins R., Adams M.B., Kirschbaum C., Carson W.P. (2010) Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91: 93–105. <http://dx.doi.org/10.1890/08-1680.1>
- Staelens J., De Schrijver A., Verheyen K., Verhoest N.E.C. (2008) Rainfall partitioning into throughfall, stemflow, and interception within a single beech (*Fagus sylvatica* L.) canopy: influence of foliation, rain event characteristics, and meteorology. *Hydrological Processes* 22: 33–45. <http://dx.doi.org/10.1002/hyp.6610>
- Sterken G.J.A.M. (1993) Analyse van de kruidvegetatie in relatie tot boomsoort en bodemkwaliteit. Erasmus internship report, Ghent University, Ghent, Belgium.
- Thimonier A., Dupouey J.L., Bost F., Becker M. (1994) Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. *New Phytologist* 126: 533–539. <http://dx.doi.org/10.1111/j.1469-8137.1994.tb04252.x>
- Thimonier A., Dupouey J.L., Timbal J. (1992) Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine plain under the influence of atmospheric deposition. *Forest Ecology and Management* 55: 149–167. [http://dx.doi.org/10.1016/0378-1127\(92\)90098-T](http://dx.doi.org/10.1016/0378-1127(92)90098-T)
- Thomaes A., De Keersmaeker L., Van Calster H., De Schrijver A., Vandekerckhove K., Verstraeten G., Verheyen K. (2012) Diverging effects of two contrasting tree species on soil and herb

- layer development in a chronosequence of post-agricultural forest. *Forest Ecology and Management* 278: 90–100. <http://dx.doi.org/10.1016/j.foreco.2012.04.026>
- Ulrich B. (1991) An ecosystem approach to soil acidification. In: Ulrich B., Summer M.E. (eds) *Soil acidity*: 28–79. New York, Springer.
- Van Calster H. (2008) Effects of changing management regimes on understorey plant communities in former coppice systems. PhD thesis, KU Leuven, Leuven, Belgium.
- Van Calster H., Baeten L., De Schrijver A., De Keersmaecker L., Rogister J.E., Verheyen K., Hermy M. (2007) Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. *Forest Ecology and Management* 241: 258–271. <http://dx.doi.org/10.1016/j.foreco.2007.01.007>
- Van Calster H., Baeten L., Verheyen K., De Keersmaecker L., Dekeyser S., Rogister J.E., Hermy M. (2008) Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. *Forest Ecology and Management* 256: 519–528. <http://dx.doi.org/10.1016/j.foreco.2008.04.042>
- Van Oijen D., Feijen M., Hommel P., Den Ouden J., DeWaal R. (2005) Effects of tree species composition on within-forest distribution of understorey species. *Applied Vegetation Science* 8: 155–166. <http://dx.doi.org/10.1111/j.1654-109X.2005.tb00641.x>
- Vande Walle I. (2007) Carbon sequestration in short-rotation forestry plantations and in Belgian forest ecosystems. PhD thesis, Ghent University, Ghent, Belgium.
- Vanguelova E.I., Benham S., Pitman R., Moffat A.J., Broadmeadow M., Nisbet T., Durrant D., Barsoum N., Wilkinson M., Bouchereau F., Hutchings T., Broadmeadow S., Crow P., Taylor P., Durrant Houston T. (2010) Chemical fluxes in time through forest ecosystems in the UK – Soil response to pollution recovery. *Environmental Pollution* 158: 1857–1869. <http://dx.doi.org/10.1016/j.envpol.2009.10.044>
- Vanhellemont M., Verheyen K. (2011) *Bos onder de Loep*. 40 jaar onderzoek in het Aelmoeseneiebos. Ghent, Academia Press.
- Verheyen K., Baeten L., De Frenne P., Bernhardt-Römermann M., Brunet J., Cornelis J., Decocq G., Dierschke H., Eriksson O., Hédl R., Heinken T., Hermy M., Hommel P., Kirby K., Naaf T., Peterken G., Petřík P., Pfadenhauer J., Van Calster H., Walther G.-R., Wulf M., Verstraeten G. (2012) Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology* 100: 352–365. <http://dx.doi.org/10.1111/j.1365-2745.2011.01928.x>
- Verstraeten A., Neirynek J., Genouw G., Cools N., Roskams P., Hens M. (2012a) Impact of declining atmospheric deposition on forest soil solution chemistry in Flanders, Belgium. *Atmospheric Environment* 62: 50–63. <http://dx.doi.org/10.1016/j.atmosenv.2012.08.017>
- Verstraeten A., Sioen G., Neirynek J., Roskams P., Hens M. (2012b) *Bosgezondheid in Vlaanderen*. Bosvitaliteitsinventaris, meetnet Intensieve Monitoring Bosecosystemen en meetstation luchtverontreiniging. Resultaten 2010–2011. Report INBO.R.2012.28. Brussel, Instituut voor Natuur- en Bosonderzoek.
- Verstraeten G., Baeten L., De Frenne P., Vanhellefont M., Thomaes A., Boonen W., Muys B., Verheyen K. (2013a) Understorey vegetation shifts following the conversion of temperate deciduous forest to spruce plantation. *Forest Ecology and Management* 289: 363–370. <http://dx.doi.org/10.1016/j.foreco.2012.10.049>
- Verstraeten G., Baeten L., Van den Broeck T., De Frenne P., Demey A., Tack W., Muys B., Verheyen K. (2013b) Temporal changes in forest plant communities at different site types. *Applied Vegetation Science* 16: 237–247. <http://dx.doi.org/10.1111/j.1654-109X.2012.01226.x>
- Vockenhuber E.A., Scherber C., Langenbruch C., Meißner M., Seidel D., Tschardt T. (2011) Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 111–119. <http://dx.doi.org/10.1016/j.ppees.2011.02.004>
- von Oheimb G., Brunet J. (2007) Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. *Acta Oecologica* 31: 229–242. <http://dx.doi.org/10.1016/j.actao.2006.12.001>
- Wickham H. (2009) *ggplot2: elegant graphics for data analysis*. New York, Springer.

Manuscript received 2 Sep. 2013; accepted in revised version 13 Dec. 2013.

Communicating Editor: François Gillet.