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Unexpected understorey community development after 30 years in ancient and post-agricultural forests

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ABSTRACT

1. Land-use change is considered one of the most radical and extensive disturbances that have influenced plant distributions and diversity patterns in forest understorey communities in much of Europe and eastern North America. In forests growing on former agricultural land, local species diversity and community differentiation among sites are generally reduced compared to ancient forests (i.e. forests with no historical record of agriculture). Yet, no study has determined how the compositional differences created by former land use change over time as the forest sites recover from former agricultural use.

2. Here we resurveyed 78 vegetation plots (half of the plots in ancient and half in post-agricultural forest) to demonstrate how three decades of forest development have changed the compositional differences between post-agricultural and ancient forest sites. The impact of land-use history and survey date was tested on two measures of species diversity and two measure of community divergence.

3. The data indicate that the imprint of former agricultural land use persisted over time, yet not through compositional stability. Parallel and strong vegetation shifts occurred in both ancient and post-agricultural forest: the species diversity decreased and local species cover strongly diverged, which indicates community drift. The observed understorey changes did thus not support the commonly accepted model of community development in post-agricultural forests, i.e. the diversity did not increase and the vegetation did not become more similar to the ancient forest vegetation over time. The changes in species composition were associated with an increase of common, competitive species at the expense of ancient forest indicator species. The source populations of ancient forest species have been gradually depleted, so the recovery of post-agricultural forests becomes even more precarious.

4. *Synthesis.* While land-use history is likely to persist as the primary predictor of local species diversity and community divergence, other environmental drivers may additionally structure

forest understorey communities and lead to biotic impoverishment and pervasive species reordering on the time scale of only decades.

Key-words: ancient forest, biodiversity balance, community drift, disturbance, forest herbs, land-use history, plant population and community dynamics, secondary forest succession, semi-permanent plots

INTRODUCTION

The extinction and colonization of species in local plant communities are major community-structuring processes that are profoundly influenced by disturbances (*sensu* Picket & White 1985; Grime 2001) and environmental changes (e.g. Smith *et al.* 2009). Yet, plant communities often show a delayed response to disturbance or environmental change because of lags in the extinction and colonization of species (Jackson & Sax 2010). Habitat degradation or destruction may directly remove local populations, but species in remnant, isolated habitat patches may experience time-delayed extinction because of a continuing negative population growth. The total number of species that ultimately becomes extinct constitutes the 'extinction debt' (Tilman *et al.* 1994; Vellend *et al.* 2006; Jackson & Sax 2009). Likewise, species colonization might be delayed after disturbance because of lag phases in the dispersal and establishment of populations, representing the colonization or immigration credit (Hanski 2000; Jackson & Sax 2009). Furthermore, chronic resource alterations (e.g. increased levels of reactive nitrogen deposition or climate change) represent pervasive environmental changes that might additionally generate gradual extinction and colonization within plant communities. Smith *et al.* (2009) predict that chronic resource alterations cause a hierarchical community response in which individual species-level responses are followed by community reordering, species loss and colonization of species that are better suited for the new environmental conditions.

Massive forest clearance for agriculture, followed by land abandonment and forest recovery, has represented one of the most radical and extensive disturbances in many landscapes in Europe and eastern North America over the past centuries (e.g. Whitney 1994; Kirby & Watkins 1998). Because land use for agriculture had largely removed the forest vegetation and because many forest herbs have a very limited colonization capacity, local (alpha) diversity in post-agricultural forest may remain reduced compared to historically continuous 'ancient' forest for decades to centuries (reviewed in Flinn & Vellend 2005; Hermy & Verheyen 2007). Beta diversity will also be suppressed in post-agricultural forests because the colonization capacity of forest herbs is strongly limited by dispersal (e.g. Matlack 1994; Verheyen *et al.* 2003) and the same suite of good dispersers of the regional pool will, consequently, be overrepresented in the local community relative to the weak dispersers (Vellend 2004; Vellend *et al.* 2007). Furthermore, the remnant vegetation in isolated ancient forest patches may lose species over time resulting from stochastic extinction or negative demographic rates, i.e. paying off their extinction debt (Vellend *et al.* 2006; Rogers *et al.* 2009). In this way, land-use history may have an overriding impact on the vegetation patterns in present-day forests (Flinn & Vellend 2005).

There is strong evidence that forest vegetation is also prone to dramatic shifts on a time scale of decades driven by the chronic alteration of environmental conditions (e.g. Thimonier *et al.* 1994; Rooney *et al.* 2004; Taverna *et al.* 2005; Wiegmann & Waller 2006; Rogers *et al.* 2008; Van Calster *et al.* 2007; Baeten *et al.* 2009a). The observed vegetation changes in the cited studies generally fit the hierarchical response framework suggested by Smith *et al.* (2009), i.e. communities are strongly reordered in terms of relative abundances and habitat specialists are largely replaced by already widespread species. The shifts are thus generally associated with biotic impoverishment and increased similarity among habitat patches, called biotic homogenization *sensu* Olden & Rooney (2006). Although forest vegetation responses to land-use history on the one hand and gradual responses to chronic environmental changes on the other hand are likely to occur simultaneously, they have never been studied and discussed collectively. The divergent ways of quantifying the two responses, i.e. land-use effects in contemporary landscapes versus temporal comparison using (semi-)permanent plots, largely account for this research gap. A combination of both approaches might, however, be particularly insightful into the patterns of successional recovery in post-agricultural sites within a backdrop of gradual forest herb community shifts.

One of the pioneer studies describing the overriding impact of land-use history on forest plant distributions was performed in forests in the western part of Belgium and northern France about 30 years ago (Hermy & Stieperaere 1981; Hermy 1985). We used topographical maps and detailed field descriptions to relocate 78 of the former vegetation plots in ancient (39 plots) and post-agricultural forest (39 plots) and we performed a resurvey of the vegetation. The data were analysed using two measures of species diversity and two measures of community divergence. We hypothesized that partial vegetation recovery from past agriculture reduced the compositional differences between post-agricultural versus ancient forest sites over time, but, at the same time, gradual changes in vegetation composition led to overall impoverishment and homogenization within and between sites, respectively.

MATERIALS AND METHODS

Study area, plot selection and forest community surveys

The studied forests are all situated in the former county of Flanders, comprising the north-western part of Belgium (western Europe). The study area is a level area with altitudes varying between 0 and 40 m a.s.l.; soil texture varies from sandy in the north to loamy in the south. The history and distribution of forests in the landscape are the result of several phases of forest progression and regression (Tack *et al.* 1993; Verheyen *et al.* 1999). The earliest traces of human impacts on the forests in Flanders go back to prehistorical times, and there is clear evidence for deforestation for agriculture and reforestation during Roman times (50 BC–350 AC) and the Middle Ages (4th century–14th century). The first regional, detailed (scale *c.* 1:12 500) land-use map was constructed around 1775 (De Ferraris map). Forest cover equalled about 12.8 % at that time, but decreased to 4.7% by 1880 (Tack *et al.* 1993). Afterwards, the forest area slightly increased again and forest cover in the present-day landscape is about 5%.

Between 1977 and 1983, M. Hermy recorded the forest vegetation in 640 vegetation plots (100–200 m²) distributed over 183 forests in the study region (Hermy 1985). The data from this survey will be referred to as the 1980 data henceforth. The percentage cover of each species in the herb layer was

estimated using Londo's decimal scale during late spring (April–first half of June). The plots were marked on topographic maps (scale 1:25 000) and additional descriptions and location sketches were recorded. Land-use history of the forest stands was reconstructed using the map of De Ferraris (1775) and the first edition (1862) and revised version (1884–1911) of the Ordnance Survey maps of Belgium. The aim of this data set was to work out a phytosociological classification of ancient and post-agricultural forest vegetation in the region (Hermy 1985). For the present study, we selected 78 plots based on phytosociological and historical-ecological criteria. First, the plots had to be situated in alluvial forest, a forest type that supports species-rich communities and is of particular concern for conservation in Europe (protected with priority in the European Habitat Directive). Second, selected plots had to be located in ancient forest, i.e. continuously forested since the oldest land-use map of De Ferraris (1775), or in forest established on former agricultural land after 1862 (first topographical map). This pragmatic classification is based on the common definition of ancient and post-agricultural forest (see Flinn & Vellend 2005), and fits the last afforestation movement in the region (see above). Third, the plots had to be in forest stands with no recent cuttings (< 10 years); this was evaluated in the field.

In late spring 2009, we relocated the 78 selected plots using the topographical maps, field descriptions and guidance of the original surveyor (M. Hermy). Half of the plots were in ancient forest stands, half in post-agricultural stands. While the plots were thus not permanently marked in the field, the procedure has proven to result in reliable temporal comparisons in previous projects (e.g. Van Calster *et al.* 2007; Baeten *et al.* 2009a). After relocating a plot, we recorded the vegetation of the herbaceous layer analogously to the old survey, i.e. we used the same plot sizes and cover scale. Individuals of the genera *Viola* and *Rubus* were not determined at the species level.

Data analysis

We applied four community measures that were proposed by Vellend (2004) in a study that determined land-use effects on the species and genetic diversity of forest herbs. Two measures of species diversity and two measures of community diversity were calculated using presence–absence data and cover data. The two measures for species diversity were the number of species in a plot, i.e. Species Richness (SR, presence–absence data) and Evenness (E, cover data). For the calculation of E we first rescaled (normalized) the percentage cover of each species so that the sum of the rescaled cover values of all species in a plot equalled 1 (NC_i: normalized cover of species i; $\Sigma NC_i = 1$). Then, E was calculated as $1 - \Sigma(NC_i)^2$. The measure E can be interpreted as the probability that two randomly chosen single-species patches that represent one percent of the total cover will belong to the same species. We used the odds ratio E/(1-E) in the statistical analyses to remove the positive skew in the distribution of E.

The first measure of community divergence was the presence-absence based Raup–Crick beta diversity (β_{RC}). This is a probabilistic measure of beta diversity that is not biased by differences in species richness among plots, i.e. it is suitable to determine changes in divergence isolated from changes in diversity. See Vellend (2004) and Vellend *et al.* (2007) for a good argumentation on this topic. The β_{RC} index gives the probability that two plots share fewer species than expected under a null model. First, the number of species shared by plots *x* and *y* with *i* and *j* species, respectively, is calculated. Then, 1000 random draws of *i* and *j* species are taken from the 'species pool', which is the collection of all species in the 78 plots. The probability of selecting a particular species is proportional

to the number of plots in which it occurred. The proportion of pairs of null communities that have the same number or more species in common than plot x and y represents the divergence between those plot ($\beta_{RC,xy}$). For a given plot, the mean of all the pairwise values against all other plots is that plot's degree of community divergence or β_{RC}. The calculation of β_{RC} for each plot was done for the 1980 data and the 2009 data separately, thus, it gives the degree of community divergence of a plot in 1980 or 2009 against all other plots in the landscape at that time.

The second measure of community divergence (F_{ST}, cover data) was a community analogue of the fixation index in population genetics (F_{ST}), which expresses the reduction in heterozygosity in a subpopulation due to genetic drift. In community terms, the index describes differences in the relative cover of species between plots, i.e. a weak correlation between the species cover in two plots indicates divergence in local abundance or 'community drift'. The divergence between two plots x and y is based on the Evenness index (see above) and is calculated as $F_{ST,xy}$ = ($E_{between}$ - E_{within})/$E_{between}$. For the pair of plots, $E_{between}$ is the Evenness index based on summed cover values of each species in the two plots. The E_{within} is simply the mean of the Evenness values for each of the two plots. The F_{ST} value for a given plot is the mean of all the pairwise values against all other plots.

We used Generalized Linear Mixed-Effects Models (GLMMs) to test the effect of former land use (ancient vs. post-agricultural) and survey year (1980 vs. 2009) on the four diversity indices. Plot identity was used as a random factor to account for the paired nature of the plots over time. Models for the response variables E/(1-E), β_{RC} and F_{ST} were fitted using the lme function of the 'nlme' libary in R (R Development Core Team 2009). Because species richness (SR) is a count variable, we applied Poisson GLMM with log link functions implemented in the lmer function in the 'lme4' library.

Analysis of Dissimilarity (ADONIS) was used to test whether the differences in community composition between the two time periods and between plots with contrasting land-use history were significant (Anderson 2001). The interaction term between land use and survey indicates whether the community composition in post-agricultural and ancient forest became more similar over time. The analysis was performed on the full untransformed data matrix, and the Jaccard distance on species cover data was used to calculate dissimilarities among plots. Calculations were done in the 'vegan' library in R. Finally, we determined which species or species strategies mainly accounted for the community changes between 1980 and 2009. First, we focused on the species that were significantly associated with ancient forest in 1980 (ancient forest species *sensu* Hermy *et al.* 1999) because those species largely account for the persistent differences in community composition between ancient and post-agricultural forest. Species associations were tested using the chi² statistic on species frequencies (cf. Hermy & Stieperaere 1981; Hermy 1985). The change in frequency of these species between 1980 and 2008 was tested with a Wilcoxon Signed-Rank test with Monte Carlo determination of the significance. Second, we calculated the Competitive, Stress tolerant and Ruderal (C-S-R) signature of each plot in 1980 and 2009 according to Hunt *et al.* (2004). The signature is a three-part numerical index (C, S and R coordinate) that represents the balance between the plant strategies (*sensu* Grime 2001) within the community based on the cover of individual species. Changes between 1980 and 2009 in ancient or post-agricultural forest were tested with paired t-tests.

RESULTS

We found 105 different species across the 78 plots in the old survey and 94 species in the new survey. Twenty-nine species were only found in the old survey and 18 new species appeared in the new survey. The ADONIS showed that land-use history was a stronger predictor for the variation in community composition among sites (F = 5.938, $P < 0.001$) than survey date (F = 3.081, $P < 0.001$). The interaction between land use and survey was not significant (F = 1.268, $P = 0.172$), i.e. the post-agricultural forest vegetation did not become more similar to the ancient forest vegetation over time.

Land-use history had a significant impact on the species diversity and community divergence (Table 1, Fig. 1). The evenness (E) and presence–absence based community divergence (β_{RC}) were reduced in post-agricultural versus ancient forest stands, while cover-based divergence (F_{ST}) was significantly higher in post-agricultural forest. Furthermore, the two measures of species diversity (evenness and species richness) decreased between 1980 and 2009. The cover-based community (F_{ST}) divergence increased over time, i.e. local species cover appears to have diverged. The species that showed the strongest shifts in plot-level cover were all generalists characterized by a competitive component in their strategy (see Figure S1 in Supporting Information). The interaction between land use and survey was never significant.

Table 1 Effect of survey (1980 vs. 2009) and land-use history (ancient vs. post-agricultural) on two measures of species diversity (SR: Species Richness; E: Evenness) and two measures of community divergence (β_{RC}: presence-absence based divergence; F_{ST}: cover-based divergence) in 78 vegetation plots in alluvial forest sites in the western part of Belgium.

	Survey			Land use			Survey × Land use	
	Effect	F/z	P	Effect	F/z	P	F/z	P
Diversity								
SR	–	-3.122	0.002		0.623	0.533	-0.630	0.529
E/(1-E)	–	5.944	0.017	–	2.911	0.092	1.753	0.190
Divergence								
β_{RC}		0.007	0.934	–	5.372	0.023	2.689	0.105
F_{ST}	+	22.408	< 0.001	+	4.560	0.036	1.138	0.290

Notes: Generalized linear mixed-models included plot identity as random factor to account for the paired nature of the data. Survey (1980 = 0; 2009 = 1) and land use (ancient = 0; post-agricultural = 1) were coded as binary variables, thus positive effects indicate higher values in 2009 or post-agricultural sites. Effects are shown if $P < 0.1$. The response variables E/(1-E) and β_{RC} were square root and log-transformed, respectively.

We identified nine forest herbs that were significantly associated with ancient forests (chi²-test P < 0.1; inset Fig. 2). Seven out of the nine ancient forest species contributed to the decline in species richness of the ancient forest sites (Fig. 2; change in frequency Z = -1.66, P = 0.05). These species disappeared on average from 31% of the plots in which they occurred in 1980. The analysis of the C-S-R signature of plots showed that the C-component significantly increased (t = 2.94, P = 0.006), while the R-component (t = -1.99, P = 0.05) and S-component (t = -1.91, P = 0.06) decreased in ancient forest (Figure S2). In post-agricultural forest, only de R component significantly decreased (t = -2.17, P = 0.04).
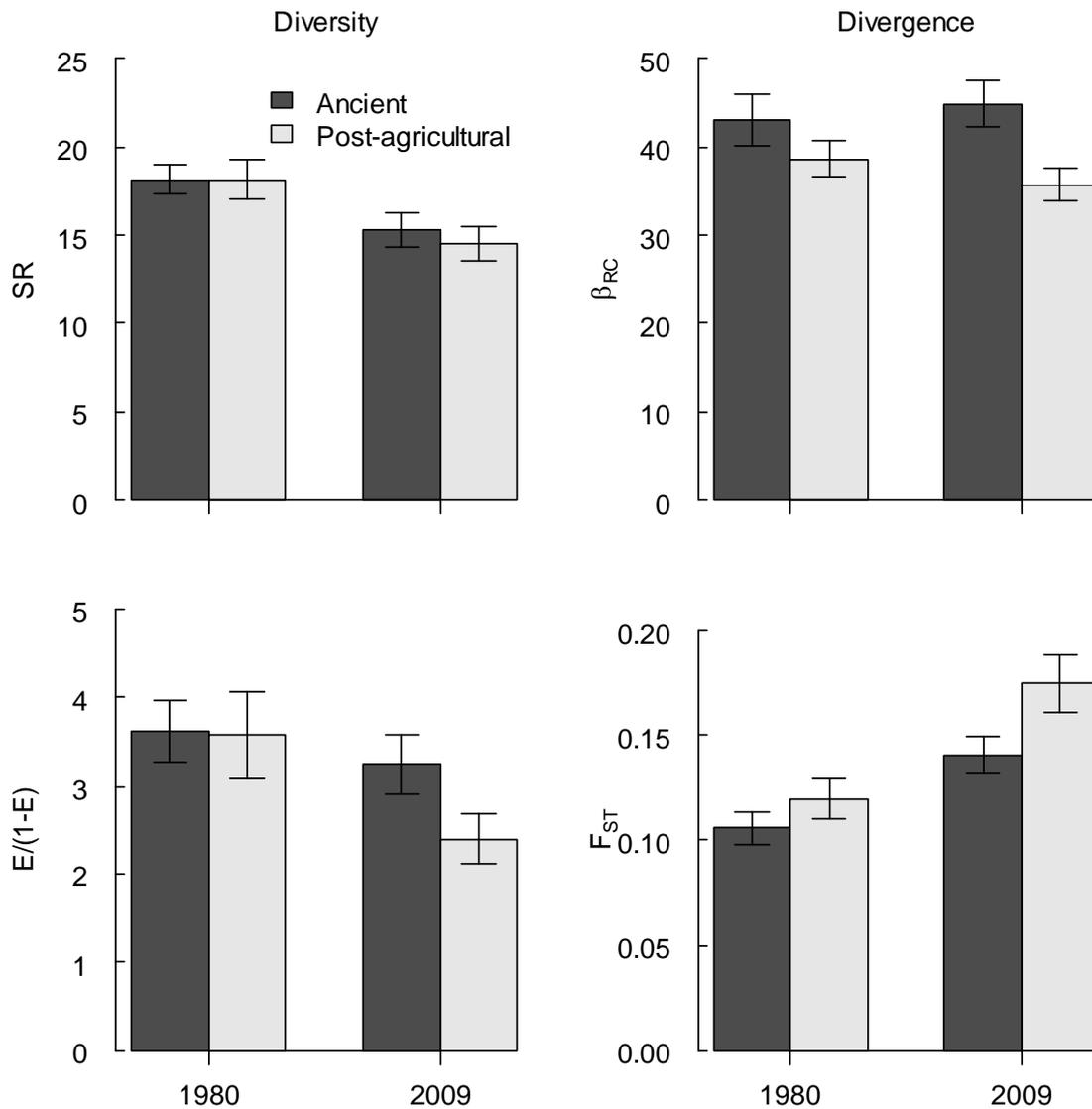

Fig. 1. Effect of land-use history and survey on the two measures of species diversity and the two measures of community divergence. SR: Species Richness; E/(1-E): odds ratio of Evenness index (E); β_{RC}: presence–absence based community divergence (Raup–Crick beta diversity); F_{ST}: cover-based community divergence. Statistical results are reported in Table 1.
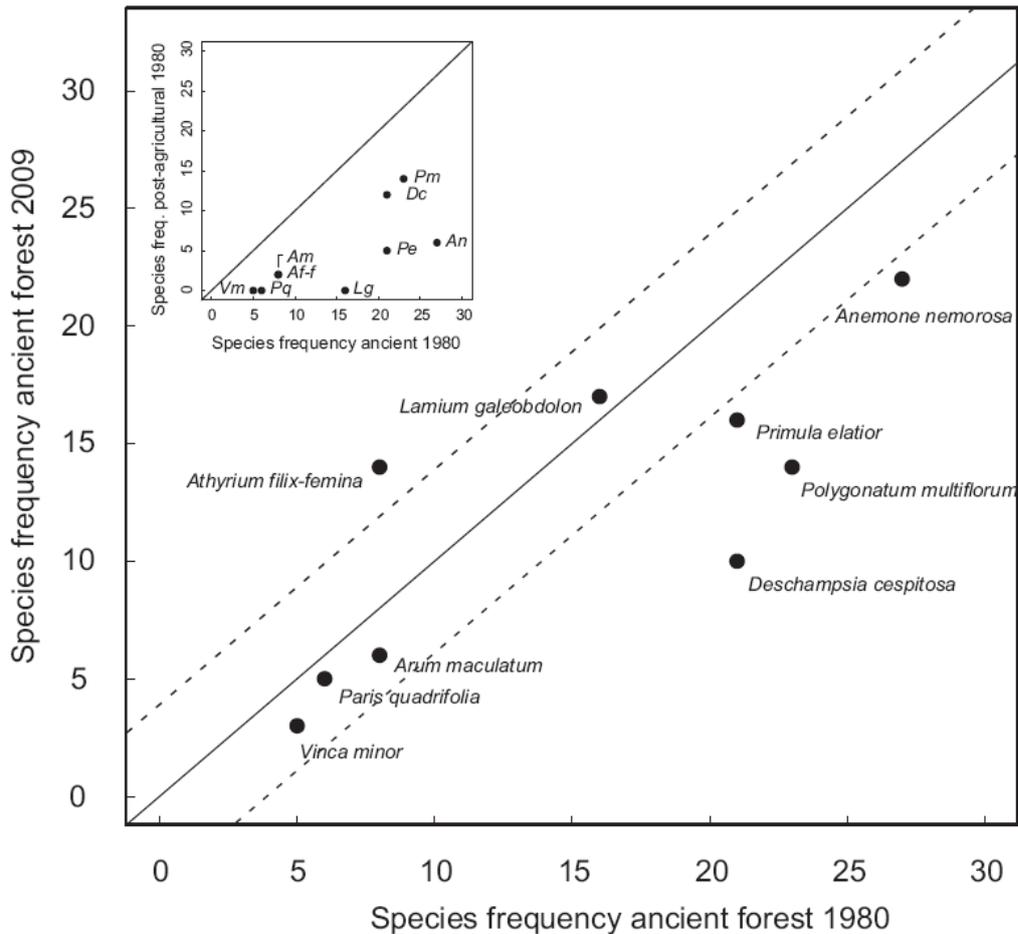
Fig. 2. Change in frequency of species that were significantly associated with ancient forest ('ancient forest species') between 1980 and 2009 (N = 39). The full line represents the 1:1 line of no change, the dashed line a change in frequency of 10 % of the 39 plots. The inset figure gives the frequency of the species (abbreviated) in ancient forest vs. post-agricultural forest in 1980.

DISCUSSION

The patterns of diversity and divergence of the forest herb layer communities were clearly related to former land use, but also changed significantly over time. Moreover, the effects of land use and survey date were additive, i.e. effect directions were concordant and interactions were never significant. The temporal shifts in post-agricultural forest vegetation thus largely parallel the shifts in ancient forest vegetation, which means that the community differences created by former land use persisted over time. Furthermore, land use was a stronger predictor of community composition than survey date, but both had a significant and additive impact on the variation in species composition among plots. Although we found gradual vegetation shifts over three decades, they do not corroborate the expected vegetation recovery after land-use change and the decrease in compositional differences between post-agricultural and ancient forest sites.

The effects of land use on species diversity and community divergence were largely in accordance with the patterns found by Vellend (2004) in forest stands in central New York (USA). Reduced beta diversity (β_{RC}) in post-agricultural forest compared to ancient forest indicates that the same suite of species tend to be overrepresented in post-agricultural sites. Vellend *et al.* (2007) suggested that selective dispersal filters constrain the pool of species that can colonize after the vegetation has been cleared away for agriculture, which creates increased similarity among post-agricultural communities, i.e. biotic homogenization (Olden & Rooney 2006). Although a differential dispersal capacity may largely account for the contrasting colonization capacity of forest herbs (reviewed in Verheyen *et al.* 2003), differences in recruitment and establishment success may additionally constrain the post-dispersal stages of colonization (Flinn 2007; Baeten *et al.* 2009b,c). We identified nine forest herbs that were significantly associated with ancient forests, of which seven were included in a European list of ancient forest indicators (Hermy *et al.* 1999). These ancient forest species are pivotal in the studied landscape as they strongly contribute to the differences in composition and beta diversity between ancient and post-agricultural forest vegetation. In contrast to β_{RC}, the divergence in relative species cover (F_{ST}) was the highest in post-agricultural forest. So, while the vegetation composition among post-agricultural sites is relatively similar, local species cover may vary considerably, i.e. species rank differently in terms of their cover among plots. The randomness of local species cover is primarily driven by 'community drift' (*sensu* Vellend 2010) and is expected particularly in biotically impoverished communities (Vellend 2004, 2010). As a suite of dispersal and establishment bottlenecks increases the proportion of ecological equivalent species in post-agricultural forest (cf. Verheyen *et al.* 2003; Vellend *et al.* 2007; Baeten *et al.* 2009b), demographic stochasticity may have partly replaced interspecific interactions in structuring local abundances (Hubbel 2001).

Species diversity, measured as species richness and evenness, significantly decreased between 1980 and 2009. This observation contradicts the widely accepted model of community development as forests recover from past agriculture, i.e. diversity gradually increasing over time (reviewed in Flinn & Vellend 2005). A decline in (native) species diversity has also been observed elsewhere in European and North American forests and was attributed to canopy succession (Brewer 1980; Rogers *et al.* 2008; Van Calster *et al.* 2008) and to gradual alterations of the environmental conditions including changes in grazing, forest management, fire regime and atmospheric deposition and the increase in non-native species invasion (e.g. Thimonier *et al.* 1994; Rooney *et al.* 2004; Taverna *et al.* 2005; Rogers *et al.* 2008; Van Calster *et al.* 2007, 2008). The cause of species decline in the present study is probably a combination of the stand maturation (e.g. increased shade) that has followed the decline of traditional, intensive management (Tack *et al.* 1993; cf. Taverna *et al.* 2005) and the desiccation and eutrophication associated with the intensification of the land use in the surrounding landscape (Lameire *et al.* 2000). The overall decline of species with ruderal component in their strategy and simultaneous increase of competitive species (Figure S2), for instance, suggest a lower disturbance level (relaxation of management) and increased nutrient availability by eutrophication (Grime 2001). Furthermore, seven out of the nine ancient forest species disappeared from on average one third of the plots between 1980 and 2009 and contributed to the decline in species richness of the ancient forest sites. The demanding nature of these forest specialists probably underlies their sensitivity to local extinction under changing habitat conditions. Species relaxation after historical forest fragmentation, i.e. paying off the extinction dept, may also contribute to the losses (Vellend *et al.* 2006; Rogers *et al.* 2009; Jackson & Sax 2009). At the same time, only two out of the nine species

colonized more than one post-agricultural plot over thirty years. A colonization credit thus still persists several decades after agricultural abandonment. As ancient forest populations appear to decline quite rapidly, source populations are progressively depleted and the slow recovery of post-agricultural forest vegetation becomes even more precarious.

The divergence among plots in terms of species composition (β_{RC}) did not change between 1980 and 2009, so forest herb layer communities did not suffer from the temporal biotic homogenization reported in other studies (e.g. Rooney *et al.* 2004; Rogers *et al.* 2008; Van Calster *et al.* 2007). Yet, the divergence in terms of local species cover (F_{ST}) did increase considerably over time, i.e. different species gained dominance in different plots. Local cover did, however, not diverge completely randomly: the species exhibiting the strongest changes in absolute cover are all characterized by a competitive component in their plant strategy *sensu* Grime (2001) and generally increased their cover (Figure S1). A common feature of those species (e.g. *Rubus fruticosus spp, Ribes rubrum, Urtica dioica, Aegopodium podagraria* and *Hedera helix*) is their capacity for rapid growth, high biomass production and fast lateral spread, which enables them to produce high shoot and root densities and to outcompete other forest herbs. Thus, although the identity of the species that increased in each plot differed, the nature of those species was relatively similar among plots. The herb layer communities in the present study appear to have entered the species reordering stage predicted by the hierarchical response framework of Smith *et al.* (2009). At this stage, a particular suite of species, here the species with stronger competitive ability, are being favoured by changing environmental conditions at the expense of others. The species reordering stage is expected to result in a subsequent phase associated with species extinctions and the immigration of generalists (Smith *et al.* 2009). Although no biotic homogenization has been observed yet, future compositional changes are to be expected.

To conclude, the overriding impact of land-use history on local species diversity and community divergence of the forest herb vegetation persisted for thirty years. Thus, unlike the commonly accepted model of community development in post-agricultural forests, species diversity and compositional similarity with ancient forest did not increase over time. The permanence of land-use legacies was not simply the result of compositional stability; we found strong and parallel declines in local species diversity and increased divergence in species cover in both ancient and post-agricultural forest sites. Jackson & Sax (2009) recently conceived the 'biodiversity balance', which is the diversity level after the extinction debt or the colonization credit following a major disturbance have been paid off (e.g. habitat fragmentation or destruction). Our results not only show that the forest communities have not yet achieved this equilibrium following the former land-use changes, but also indicate that the overall diversity level in both ancient and post-agricultural forest has strongly declined in a time span of decades due to biotic impoverishment and profound species reordering. Although knowledge about the former land use enables us to largely explain the distributional patterns and cover of species in contemporary landscapes, the resurvey of historical records provides important additional insights into how present-day plant communities were structured during the past decades and how they might shift in the future.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1 Plot-level changes in species cover (%) for a selection of six species that showed the largest mean absolute change in plot-level cover between 1980 and 2009.

Figure S2 Changes of the C-S-R signature of vegetation in ancient and post-agricultural forest between 1980 and 2009.

Table S1 Species-level changes in frequency and cover between 1980 and 2009

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Figure S1 Plot-level changes in species cover (%) for a selection of six species that showed the largest mean absolute change in plot-level cover between 1980 and 2009. The strategy of the species is reported within parenthesis (Hodgson *et al.* 1995). The "N plots" gives the total number of plots in which the species occurred (total number = 78) in at least one of the two survey years (1980 or 2009).
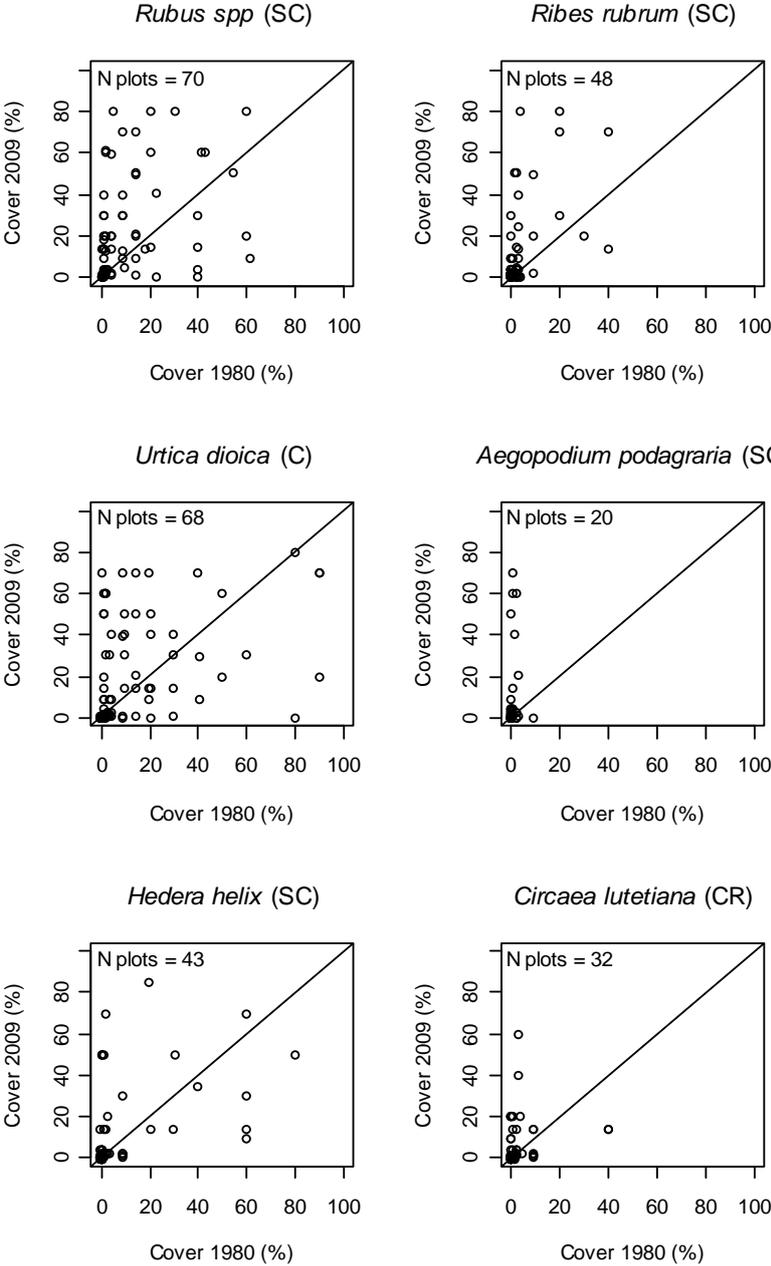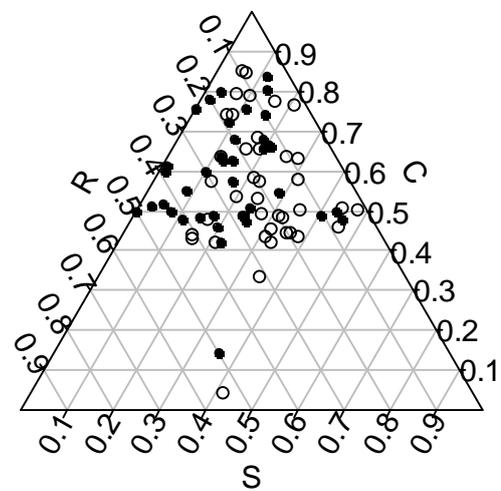

Reference: Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. (1995) The electronic comparative plant ecology. Chapman & Hall, London.

Figure S2 Changes between the C-S-R signature of vegetation in 1980 (open circles) and 2009 (filled circles). The left figure shows the plots in ancient forest, the right figure in post-agricultural forest. The C-S-R signature of a plot is a three-part numerical index (C, S and R coordinate) that represents the balance between the plant strategies (*sensu* Grime 2001) within the community based on the cover of individual species. The signature was calculated according to Hunt et al. (2004). For ancient forest vegetation, a paired t-test showed that the C-component increased (t = 2.94, *P* = 0.006) at the expense of the R-component (t = -1.99, *P* = 0.05) and S-component (t = -1.91, *P* = 0.06). For post-agricultural vegetation, only de R component significantly decreased (t = -2.17, *P* = 0.04).
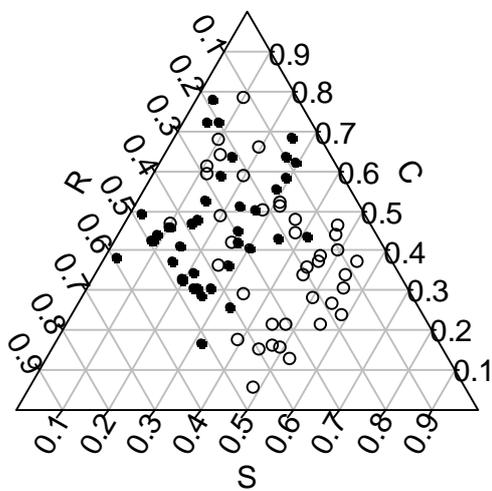
Ancient forest   Post-agricultural forest

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*Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P. & Askew, A.P. (2004) A new practical tool for deriving a functional signature for herbaceous vegetation. Applied Vegetation Science, **7**, 163-170.*

Table S1 Species-level changes in frequency and cover between 1980 and 2009. Only species occurring in 10 % of the plots in the entire dataset (1980 and 2009 data) are reported.

Species	Frequency		Cover	
	1980	2009	1980	2009
Rubus fruticosus agg.	70	69	12	23
Urtica dioica	68	63	17	27
Poa trivialis	53	31	2	3
Glechoma hederacea	51	54	13	12
Geum urbanum	51	45	1	3
Filipendula ulmaria	49	24	4	2
Moehringia trinervia	48	31	2	2
Galium aparine	47	56	2	3
Galeopsis tetrahit	46	36	1	1
Cardamine pratensis	43	12	2	3
Cirsium palustris	40	11	1	1
Polygonatum multiflorum	37	21	2	1
Rumex sanguineus	37	18	1	1
Ribes rubrum	33	48	8	16
Anemone nemorosa	33	34	27	15
Deschampsia cespitosa	33	18	6	5
Adoxa moschatellina	32	32	4	5
Angelica sylvestris	27	22	1	2
Primula elatior	27	21	4	3
Hedera helix	26	43	20	17
Stachys sylvatica	26	28	2	1
Circaea lutetiana	25	32	7	10
Viola spp	23	10	1	2
Lonicera periclymenum	22	25	1	2
Valeriana officinalis	21	7	1	2
Ajuga reptans	19	13	1	2
Holcus lanatus	19	9	4	4
Scrophularia nodosa	19	8	1	1
Carex sylvatica	18	18	2	1
Carex remota	17	18	1	8
Lamium galeobdolon	16	18	36	23
Humulus lupulus	16	15	4	1
Symphytum officinale	15	13	1	2
Aegopodium podagraria	13	20	2	18
Listera ovata	13	3	2	1
Lysimachia vulgaris	13	2	2	2
Iris pseudoacorus	12	9	1	1
Lysimachia palustre	12	6	1	1
Galium palustre	12	5	1	1
Athyrium filix-femina	10	23	2	1
Arum maculatum	10	7	2	1

Solanum dulcamara	10	2	2	2
Geranium robertianum	9	13	1	2
Ranunculus repens	9	6	3	1
Ornithogalum umbellatum	9	3	1	1
Brachypodium sylvaticum	9	2	2	2
Poa nemoralis	8	1	1	1
Heracleaum sphondylium	7	7	1	1
Paris quadrifolia	6	6	2	4
Lasana communis	5	7	1	1
Scutellaria galericulata	5	4	3	1
Taraxacum officinalis agg.	5	4	1	1
Carex elongata	5	3	1	1
Vinca minor	5	3	13	33
Dryopteris dilatata	4	27	1	4
Dryopteris carthusiana	4	8	3	1
Epipactis helleborine	3	9	1	1
Juncus effusus	3	8	1	1
Dryopteris filix-mas	3	7	1	1