

## Do drivers of forestry vehicles also drive herb layer changes (1970-2015) in a temperate forest with contrasting habitat and management conditions?

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### Abstract :

1. Managing ecosystems effectively for the maintenance of biodiversity and ecosystem functions and services requires to understand how these ecosystems are changing and what are the drivers behind these changes. The resurvey of plant communities sampled some decades ago is increasingly used for this purpose.

2. We used a life history trait-based approach to test a number of hypothesized drivers behind decadal changes (1970-2015) in the herb layer of an ancient broadleaved lowland forest exhibiting contrasted soil and management types, whilst minimizing potential relocation and observer errors.

3. Process-based hypotheses were tested using paired comparisons (old vs new records) of community weighted means and conditional inference classification trees for a number of traits across soil and management types. We then investigated how these processes impacted species composition and diversity within stands, among stands and at the entire forest scale, using metrics of taxonomic, functional and phylogenetic diversity.

4. Though they have been continuously managed as regular high forest, managed stands experienced more pronounced vegetation changes than those left unmanaged. This could be directly or indirectly related to modifications in forest harvesting practices since 1970, via light availability at the forest floor, soil disturbance and local N deposition.

5. While forest specialists increased their abundance over the entire forest, managed stands showed the strongest compositional changes, especially on the soil types that were more susceptible to compaction. Increasingly heavy forestry vehicles that drive more frequently across forests stands, likely generate micro-habitats suitable for ferns, graminoids and N-demanding forbs and also act as dispersal agents.

6. Species richness of vascular plants increased at both stand ( $\alpha$ -diversity) and forest ( $\gamma$ -diversity) scales, due to the non-random, directional colonization by the same suite of species, causing compositional, functional and phylogenetic homogenisation among habitats (i.e. decreased  $\beta$ -diversity).

7. Synthesis- Forest management, via the repeated passing of heavy forestry vehicles, emerged as the

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key driver of local vegetation changes. By altering canopy structure, it also increased the vulnerability of understories to climate warming and atmospheric deposits. Changes were not only taxonomic, but also functional, suggesting long-term effects on ecosystem functioning and thus deserve attention from forest managers and conservationists.

**Keywords** : Biotic homogenization, Environmental changes, Forest management, Habitat filter, Light availability, Plant species diversity, Soil disturbance, Vegetation resurvey

## INTRODUCTION

Developing appropriate strategies for the effective conservation of biodiversity and to maintain ecosystem functions and services has become a priority target. For this purpose, it is important to document and understand how ecosystems are changing and what are the drivers of these changes. Over the last decade, plant ecologists increasingly made profit of historical data to quantify long-term changes in forest vegetation, by resurveying georeferenced historical plots some decades after a first vegetation record (e.g. Smart et al 2006, Rogers et al. 2008, Keith et al. 2009, Verheyen et al. 2012, Bernhardt-Römermann et al. 2015, Verheyen et al. 2017). In this study we use a life history trait-based approach to investigate the drivers behind decadal changes (1970-2015) in the herb layer of the broadleaved forest of Compiègne (N France), the third biggest lowland forest in France, which has continuously existed since the end of the 5<sup>th</sup> century.

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While a number of legacy studies evidenced declines in local ( $\alpha$ -diversity) and regional ( $\gamma$ -diversity) species richness (e.g. Rogers et al. 2008, Baeten et al. 2012), others found no significant species loss (e.g. Naaf & Wulf 2010) or even an increased species richness (e.g. Smart et al. 2006, Keith et al. 2009). Both initial site conditions and interactions between different drivers may explain these contrasted results (Naaf & Kolk 2016). Here, we focus on a single big forest with a very well-known history to avoid some important biases inherent to multi-site resurvey studies, such as, for example, interregional difference in landscape context and histories, and site-to-site variations in natural (e.g. windthrows) and artificial (e.g. management) disturbances. Furthermore, since our studied forest encompasses different soil and management types, we are able to decouple their respective effects on the observed vegetation changes.

A constant result among resurvey studies is the increased compositional similarity ( $\beta$ -diversity) across sites, mostly due to the increased importance of habitat generalists at the expense of more specialized species (Rooney et al. 2004, Smart et al. 2006, Van Calster et al. 2007, Rogers et al. 2008, Verheyen et al. 2012, Bernhardt-Römermann et al. 2015, Durak & Holeska 2015, Li & Waller 2015, Savage & Vellend 2015, Heinrichs & Schmidt 2017). However, these studies are often biased by the metric used for quantifying  $\beta$ -diversity, which is not independent from species richness (Naaf & Wulf 2010, Baeten et al. 2012). In this study, we quantify changes in  $\beta$ -diversity among local communities using unbiased metrics that allow us to disentangle the replacement of some species by others (i.e., turnover) from the gain or loss of some species (i.e., nestedness) (Baselga 2010).

Recent vegetation changes in forest have been attributed to a range of environmental drivers acting at different spatial scales, which have often been studied separately from each other (Table 1). Climate warming as a global driver, has been shown causing a thermophilization of the forest herb layer (Naaf & Kolk 2016, Helm, Mirtl & Dirnböck 2017). Among regional drivers, atmospheric N deposits were found to promote ruderal, nitrogen-demanding and acid-tolerant species at the expense of oligotrophic species (Diekmann et al. 1999, Lameire, Hermy & Honnay

2000, Van Calster et al. 2007, Heinrichs & Schmidt 2017), an effect more likely to occur on acid than on base-rich soils (Baeten et al. 2009, Naaf & Kolk 2016). Increased ungulate density was also found to be an important driver of forest vegetation changes, including overbrowsing on palatable plants and the spread of endo- and epi-zoochorous species (Diekmann et al. 1999, Côté et al. 2004, Bernhardt-Römermann et al. 2015).

Local drivers include forest management, which has been mostly assessed via the type of silviculture (e.g. coppice-with-standards, regular high forest) and its effect on overstory structure and composition (e.g. Decocq et al. 2004, van Calster et al. 2007). In comparison, the recent mechanization of silviculture has received little attention despite the use of heavier and heavier forestry vehicles (e.g., skidders, forwarders, harvesters) which imply the creation of skid trails across forest stands with strong impacts on soil physical properties and the ground vegetation (Buckley et al. 2003, Avon, Dumas & Bergès 2013, Cambi et al. 2015). Changes in overstory features can occur independently from management. For example, the invasive spread of *Prunus serotina* on nutrient-poor soils (i.e. podzols) was found to favour shade-tolerant, nitrogen-demanding species, at the expense of light-demanding and oligotrophic species (Jauni & Ramula 2015). In unmanaged stands, canopy closure and the increased importance of common beech have been shown to promote species that are able to cope both with shade and a thick litter layer (i.e. forest specialists; Verheyen et al. 2012, Naaf & Kolk 2016). Local factors may not only be better predictors of local species assemblages than regional and global factors (Valdés et al. 2015), but also exacerbate or mitigate the effects of regional or global factors (e.g. climate warming; De Frenne et al. 2013).

In this study, we assess whether recent changes in harvesting practices did impact, alone or in combination with other environmental drivers, understory plant communities and whether this impact differs among soil types. More specifically, we test the following process-based hypotheses:

**H1:** Changes in plant traits within the herb layer are mostly affected in managed stands, due to greater canopy openness and soil disturbance, and can be explained by a combination of drivers acting at global, regional and local scales as summarized in Table 1.

**H2:** Changes in plant traits in response to management depend upon initial soil conditions. They are more important on soils which are more susceptible to compaction (e.g. luvisols, gleysols) or where the tree canopy is already open (e.g. podzols) (Table 1).

**H3:** Taxonomic diversity, associated with an increase in both functional and phylogenetic diversity, will increase in managed stands through the gain of the same suite of generalist species under uniform silviculture practices. Conversely, we predict a decrease in taxonomic and phylogenetic diversity in unmanaged stands due to trait convergence whereby light-demanding generalists are replaced by shade-tolerant forest specialists, in turn causing decreased functional diversity.

**H4:** if H3 is true, then both managed and unmanaged stands experienced taxonomic homogenization (i.e. decreased  $\beta$ -diversity), predominantly due to nestedness in managed stands (gain of the same suite of species) and to turnover in unmanaged stands (replacement of light-demanding by shade-tolerant species). This taxonomic homogenization will in turn cause a phylogenetic and functional homogenization, which scales up to the entire forest.

To test these four hypotheses, we resurveyed semi-permanent plots over different soil types in a deciduous forest which was continuously managed as a high forest through historical times. To single out the role of silviculture, we compared managed stands to stands left unmanaged since ca. 45 years on the same soil type.

## METHODS

### Study site

The ancient forest of Compiègne (49°24'54"N, 2°49'23"E, altitude: 31-152 m), in north France, extends over ca. 14,000 ha. The climate is sub-oceanic with mean annual temperature and annual rainfall of 10°C and 610 mm, respectively. The geological substrate consists of Paleocene and Eocene sand and limestone, locally covered by quaternary loess or drift sand. The soils are mostly cambisols, luvisols and podzols (FAO classification); waterlogged soils (gleysols) can be found in depressions along several small streams.

The forest has existed continuously since the end of the 5<sup>th</sup> century. It was used for royal and imperial hunting until 1870, and today it is still used for red deer stag-hunting. The major part of the forest has thus been managed as a high forest for centuries. Moreover, grazing by livestock and horses was a common practice until the 17<sup>th</sup> century. The forest has thus been an open woodland until the mid 19<sup>th</sup> century. Then, the canopy progressively closed but became open again following the overexploitation crises associated with the two world wars.

Ungulate densities considerably increased over the last few decades: while they were absent just after WWII, the number of red deer (*Cervus elaphus*) increased from <100 in the 1950s over 500 in the 1980s to ca. 800 since the 1990s. Roe deer (*Capreolus capreolus*) and wild boars (*Sus scrofa*) started to establish in the early 1980s to reach 150 and 330 individuals, respectively, since the 1990s.

The current vegetation is a closed-canopy temperate deciduous forest dominated by common beech (*Fagus sylvatica* L., 46%) and oaks (*Quercus robur* L., 27%; *Quercus petraea* L., 7%), except on podzols where Scots pine (*Pinus sylvestris* L.) has been largely planted during the 19<sup>th</sup> century, and waterlogged soils where ash (*Fraxinus excelsior* L.) and black alder (*Alnus glutinosa* L.) dominate the canopy. Since 1970, the American black cherry (*Prunus serotina* Ehrh.) is reported as an invasive tree species, but its first introduction would date back from the mid 19<sup>th</sup> century; it currently

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occurs in ca. 80% of the forest stands, as single trees to pure stands, especially on nutrient-poor soils (e.g. podzols).

The forest is uniformly managed as a regular high forest of beech and oak, and silviculture has intensified in the last two decades. Managed stands are thinned every 4-8 years and the final harvest occurs by clear cutting at the age of 90-110 (beech) to 140-180 (oak) years, followed by artificial plantations or natural regeneration. Two nature reserves covering 126 ha and 130 ha have been created in the mid 1970s, where no significant management is conducted and where the oldest trees are more than 400 years old.

#### **Old and new vegetation surveys**

In 1970, a vegetation survey of the Compiègne forest was carried out by a senior botanist (Tombal, 1972). As the original aim was to provide a phytosociological typology of the forest vegetation, plot location was subjectively chosen so that the ground vegetation was homogeneous, and the forest stands were representative of major habitat types within the forest and relatively undisturbed. The author compiled 139 phytosociological relevés, which were distributed among five categories: (1) lightly managed old-growth oak stands on luvisols:  $n= 28$ , (2) extensively managed oak-beech stands on luvisols:  $n= 22$ , (3) managed oak stands on podzols:  $n= 29$ , (4) managed broadleaf stands (e.g. oak, beech, ash, maple, wild cherry, lime) on cambisols:  $n= 34$ , and (5) managed ash-alder stands on waterlogged soils:  $n= 26$ . Relevés were done in temporary plots of 800 m<sup>2</sup>. For each relevé, he exhaustively recorded all vascular plant species within each vegetation layer (tree: >7m, shrub: 1-7m, herb<1m), scored their respective cover-abundance using the Braun-Blanquet scale, and visually estimated the total vegetation cover for each layer (%).



Two of us (DCK, GD) implemented a resurvey in 2015, using the same method (plot size, season) as Tombal in order to maximize reliability of the comparison between the two surveys. Semi-permanent plots were relocated based on (i) the geographic information about plot location in Tombal (1972), (ii) plot elevation, slope, aspect, soil type and local topography, (iii) tree and shrub composition. Of the 139 plots, 61 were either impossible to relocate or located in a recent clear-cut. We thus retained 78 plots, with no stand (i.e. management unit) containing more than one plot.

### **Data preparation**

We focused our analyses on the herb layer (including tree and shrub saplings), whilst overstories (shrub and tree layers) were used as environmental descriptors. We standardized species nomenclature according to Lambinon et al. (1992). Fuzzy taxa were agglomerated at the superspecies level (e.g. *Rubus fruticosus* agg., *Taraxacum officinale* agg.).

To deal with potential biases inherent to resurvey studies (Verheyen et al. 2017), we built two sets of data matrices. A first one kept all species with their original abundance-dominance score from the two surveys (hereafter MAX matrices); the differences between the two surveys may be overestimated (Verheyen et al., 2017) and thus are considered as maximal. In the second set (MIN matrices), we did not alter the old survey either, but modified the new relevés so that: (i) newly recorded species with a low cover-abundance score (i.e., i or + on the Braun-Blanquet scale) were deleted; (ii) species with a low cover-abundance score in the old relevé which were not retrieved during the resurvey were added with their original score; (iii) when the cover-abundance of a given species departed less than two scale units between the old and the new relevé, we replaced the value from the resurvey by the one of the old survey (+ vs. 1 became + in both relevés; 2 vs. 1 became 2, etc.). The first two corrections accounted for potential plot relocation error and/or species missed by the surveyors (Verheyen et al. 2017), and the third one for inter-surveyor difference in the

visual estimation of species' cover-abundance (Morrison 2016). By using MIN matrices we expect to underestimate true vegetation changes between the two surveys.

In further analyses, "old" relevés were paired with their corresponding "new" relevés, and all cover-abundance values were converted into numerical values using the ordinal scale of van der Maarel (1979).

### **Hypothesis testing and data analysis**

All statistical analyses were run for the entire data set (forest scale) and for each soil/management type separately, using successively the MAX and MIN matrices. To disentangle the effect of management from habitat influence on vegetation changes, we compared, on the first hand, unmanaged (reserves;  $n=11$ ) with managed stands on the same soil type (luvisols;  $n=23$ ) and, on the second hand, managed stands across the four soil types: luvisols, cambisols ( $n=17$ ), podzols ( $n=14$ ) and gleysols ( $n=13$ ). Whenever a statistical test was significant ( $P<0.05$ ) for both MAX and MIN matrices, we considered it reflecting a significant ecological change; whenever statistical significance was achieved with either MAX or MIN, we considered it reflected an ecological trend.

***Trait-based approach of drivers behind vegetation changes*** - To test for the hypothesized processes behind vegetation changes (**H1** and **H2**; Table 1), we derived a number of explanatory variables from the vegetation records by computing for the herb layer community only:

- cover-abundance weighted means of Ellenberg's indicator values (EIV; Ellenberg et al. 2001) for light (EIV\_L), temperature (EIV\_T), continentality (EIV\_K), soil pH (EIV\_R), soil nutrient (EIV\_N), soil moisture (EIV\_F), and browsing attractiveness (EIV\_BA; Ellenberg 1988).

- the proportion of dispersal modes, as extracted from LEDA database (Kleyer et al. 2008).
- the CSR signature of the herb community (Hunt et al. 2004).
- the community specialization index (CSI) which was computed as  $(\Sigma S + 3\Sigma G) / (\Sigma S + \Sigma G)$ , where  $\Sigma S$  and  $\Sigma G$  is the sum of cover-abundance values of forest specialists (i.e. species occurring only in forest habitats) and generalists (i.e. species whose primary habitat is not forest), respectively (Jamoneau et al. 2011). By weighting generalists by 3, CSI increases when the relative percent cover of generalists increases relative to specialists.

Overstory features were quantified using (i) the total cover of the tree layer (R%T), the shrub layer (R%S) and the cumulated cover of tree and shrub layers (R%TS) as visually estimated in the field; (ii) the cover-weighted mean of shade-casting ability (SCA) and litter quality (LQ) indices of individual overstory species (Hermy 1985); (iii) the relative cover of each major tree species in the canopy.

Changes in traits between the two surveys were tested using paired *t*-tests for all quantitative traits (EIV), the CSI and the CSR signature; and Wilcoxon rank tests for each category (%) of dispersal modes. To further test whether plant species traits responding to forest management (e.g. canopy openness through EIV\_L, soil compaction through EIV\_F) are more important than traits responding to regional (e.g. increased ungulate density through EIV\_BA) and global (e.g. climate warming EIV\_T) drivers, we used conditional inference classification trees (CICT) and all above mentioned traits. This method allows to partition species into homogeneous groups with respect to changes in frequency of traits between the two surveys while accounting for nonlinear hierarchical relationships, coping with missing values, and dealing with categorical, ordinal and quantitative data (Hothorn, Hornik & Zeileis 2006). All traits are statistically tested in each split of the tree using a permutation procedure, and the trait that best discriminates between the two groups of species is retained. The procedure continues until no trait significantly discriminates between species.

**Changes in community  $\alpha$ -diversity** - We tested for changes in the taxonomic, functional, and phylogenetic components of  $\alpha$ -diversity (**H3**), by comparing the old and new relevés with a paired *t*-test. For this purpose, we computed:

- four indices of taxonomic diversity: species richness (*S*), Simpson' diversity (*D*), Shannon's evenness (*H'*), and Pielou's equitability ( $J' = H' / \ln S$ );

- four indices of functional diversity: Rao's Q quadratic entropy (*RaoQ*), functional richness (*FRic*), functional evenness (*FEve*), and functional divergence (*FDiv*) (Laliberté & Legendre 2010; Mouchet et al. 2010; see Appendix S1 for more details). For this purpose, we followed the leaf-height-seed (LHS) ecology strategy scheme (i.e., a combination of three ecologically important traits: specific leaf area (SLA), seed mass and plant maximal height; Westoby 1998). Values for these life-history traits were extracted from LEDA (Kleyer et al. 2008) database.

- four indices of phylogenetic diversity indices (Helmus et al. 2007): Faith's phylogenetic diversity index (*PD*), phylogenetic species variability (*PSV*), phylogenetic species richness (*PSR*), and phylogenetic species evenness (*PSE*) (Appendix S1).

Functional and phylogenetic diversity indices were computed using the packages 'FD' and 'pez' (Pearse et al. 2015), respectively, in R v. 3.1.1 (R Core Team 2013).

**Community homogenization** - To test for taxonomic, functional, and phylogenetic shift over time and temporal changes in  $\beta$ -diversity (**H4**), we ran distance-based tests using Bray-Curtis distances and Jaccard-derived functional (based on volume of convex hulls intersections in a multidimensional functional space; Villéger, Novack-Gottshal & Mouillot 2011) and phylogenetic distances (Leprieur et al. 2012), respectively. We ran a principal coordinates analysis (PCoA) of each distance matrix and then tested for:

- changes in overall diversity between the two surveys, reflected by a difference in the position of the centroid (PERMANOVA; Anderson & Walsh 2013). For taxonomic diversity, the test was followed by an Indicator species analysis (ISA; 9999 permutations) to determine which species were more frequent/abundant in the old ('losers') and new ('winners') relevés (De Caceres & Legendre 2009).

- changes in  $\beta$ -diversity between the two surveys, reflected by a difference in dispersion of the relevés around the centroid (PERMDISP2; Anderson, Ellingsen & McArdle 2006). Then, to quantify the relative importance of nestedness and turnover in  $\beta$ -diversity changes between the two surveys, we further partitioned taxonomic, functional, and phylogenetic  $\beta$ -diversity following Baselga (2012), Villéger, Grenouillet & Brosse (2013) and Leprieur et al (2012), respectively:

$$\beta_{jne} = \beta_{jac} - \beta_{jtu}$$

where  $\beta_{jne}$ ,  $\beta_{jac}$ , and  $\beta_{jtu}$  express nestedness, total dissimilarity (i.e., Jaccard index), and turnover, respectively. For each relevé, we calculated the taxonomic, functional (using the three LHS traits) and phylogenetic dissimilarity between the old and new survey, considering the turnover and nestedness components of temporal changes, and the sum of both values (overall changes). Total dissimilarity, nestedness and turnover values were compared among soil/management types using a paired *t*-test.

We used the following R functions: *betadisper*, *adonis* and *permutest* in *vegan* library (Oksanen et al. 2012), *beta.pair*, *phylo.beta.pair* and *functional.beta.pair* in *betapart* package (Baselga & Orme 2012), *multipatt* in *indicspecies* package (De Caceres & Legendre 2009), and *ctree* in *party* package (Hothorn et al. 2006).

## RESULTS

A total of 159 and 201 species were recorded within the herb layer of 78 plots in 1970 and 2015, respectively (Table S1). Twenty-six species of the original species were not retrieved, of which 19 (73%) were recorded in only one plot with very few individuals and none was found in more than 3 plots. Sixty-eight species were newly found in 2015, of which 39 (57%) were found in at least 3 plots, the most frequent being *Viola reichenbachiana* (17 plots), *Sorbus aucuparia* (16), *Paris quadrifolia* (11), *Lapsana communis* (10) and *Allium ursinum* (8). Of the 227 herb species recorded during the resurvey (all kept in MAX matrices), 180 were retained to build MIN matrices. Hereafter, we show results from MAX matrices; they only marginally differ from results obtained with MIN matrices, which are shown as Supplementary material.

### Changes in plant traits

In overstories, the cover-abundance of shade-casting tree species (*Fagus sylvatica*, *Carpinus betulus*, *Acer pseudoplatanus*) increased across soil types (except on gleysols), and particularly in unmanaged stands, which also experienced an increased total cover of the tree layer (Table 2). In contrast, the total tree cover remained unchanged or even decreased in managed stand. Consistently, SCA remained unchanged at the plot scale (except on podzols: increase). The invasive *Prunus serotina* significantly spread in reserves and on podzols, and this was associated with an increased LQ. *Ulmus minor* almost disappeared from the canopy on gleysols, which also experienced a decreased LQ.

At the scale of the entire forest, EIV\_F, N and BA of the herb layer increased, whilst the CSR signature shifted from S- to R-strategy (Table 3; Table S2). The proportion of anemochores and hydrochores strongly increased at the expense of myrmecochores. These results are mostly explained by changes in managed stands on luvisols, where there was also an increased EIV\_L, T, K

and R, an increased CSI, and a decreased proportion of endozoochores. In contrast, in unmanaged stands there was a trend towards lower EIV\_L but higher EIV\_BA and proportion of myrmecochores. The herb layer of managed stands on soil types other than luvisols were less affected by changes. Podzols showed increased EIV\_R, N and BA, but decreased EIV\_L, and an increased proportion of endozoochores. Cambisols underwent an increase in EIV\_F, N and BA, and proportion of S-strategists. Gleysols showed a decreased EIV\_R.

Despite these changes in community-weighted means of trait values, a restricted set of traits significantly discriminates between winners and the other species (Fig. 1; Fig. S1). In managed stands and thus at the entire forest scale, the most discriminating trait was light requirement (EIV\_L): winners were shade-tolerant species in the whole forest (EIV\_L $\leq$ 4 and  $\leq$ 6 for the first two divisions; Fig. 1a, Fig. S1a) and in managed stands on luvisols, cambisols and gleysols (EIV\_L $\leq$  5, 4 and 6, respectively; Fig. 1c,e,f, Fig. S1c,e,f). On gleysols, winners tended to include more hygrophilic species (EIV\_F $>$ 8). Species most prone to local extinction were light-demanding species (EIV\_L $>$ 6) with heavy seeds ( $>$ 9mg) at the entire forest scale (Fig. 1a) and generalist herbs in reserves (Fig. 1b).

### Changes in community $\alpha$ -diversity

Overall,  $S$ ,  $D$ , and  $H'$  increased between 1970 to 2015, independently from management and soil type (Table 4; Table S3).  $S$  increased more in managed stands than in reserves (+25.3 vs +15.0, on average), but the former were already more species-rich in 1970 (12.8 vs 7.1). Among managed stands, the species gain increased from podzols, through luvisols, gleysols to cambisols.

$FRic$  increased irrespective of the management and soil type, as a probable effect of increased species richness in most cases, since among richness-independent indices, only  $RaoQ$  significantly increased in reserves and on podzols.  $FDiv$  and  $FEve$  tended to remain unchanged across management and soil types.

*PD* and *PSR* increased irrespective of the management and soil type. *PD* increased more in managed stands than in reserves, whilst *PSR* increased mainly in reserves. *PSE* and *PSV* tended to remain unchanged across management and soil types.

### Changes in community $\beta$ -diversity

At the entire forest scale, species composition experienced both a significant shift (i.e. different position of the centroid in the PCoA diagram) and homogenization (i.e. lower dispersion of relevés around the centroid) (Fig. 2a; Fig. S2Aa). This shift and homogenisation not only affected species composition, but also functional (Figs. S2Ba,g) and phylogenetic diversity (Figs. S2Ca,g). The observed taxonomic dissimilarity was almost equally due to nestedness and turnover, whilst the phylogenetic and functional dissimilarity was mostly due to nestedness (Fig. 3a; Fig. S3a). This means that new species have colonized the plots since 1970, introducing new phyla with new traits, while fewer established species went extinct. Consistently, the ISA returned 25 and 74 species as “winners” with MIN and MAX matrices, respectively, but no indicator species for “losers” (Table S1). Winners mostly include ferns, tree saplings, shade-avoiders and shade-tolerant forbs.

Apart from gleysols, there was a significant shift in both species composition and community phylogenetics across all management and soil types, which was associated with a shift in functional composition (significant in managed stands on luvisols and cambisols, trend in reserves and on podzols; Figs. 2b-f; Figs. S2Ab-f). These shifts occurred without homogenization except on cambisols which experienced taxonomic, phylogenetic and functional homogenization. Species composition became more homogeneous in unmanaged stands but with little impact on functional  $\beta$ -diversity and no change in phylogenetic  $\beta$ -diversity. Nestedness and turnover more or less equally explained changes in taxonomic  $\beta$ -diversity between the two surveys across management and soil types, except on gleysols where turnover predominated (Fig. 3b-e; Fig. S3b-e). In contrast, phylogenetic and



functional  $\beta$ -diversity were mostly due to nestedness, irrespective of management and soil type. Winners were mostly tree saplings in reserves (Table S1), whilst in managed stands, winners further included ferns, graminoids, shade-avoiders and nitrogen-demanding shade-tolerant forbs. Podzols, like reserves, experienced a spectacular increase of the cover-abundance of *P. serotina* saplings.

## DISCUSSION

By avoiding biases associated to multi-sites comparisons and applying the same analyses to MIN and MAX matrices, our results likely comprise the range of errors associated to relocation and observer biases (Kopecky & Macek 2015, Kapfer et al. 2017, Verheyen et al. 2017). They reveal far stronger vegetation changes in managed than in unmanaged stands over the last forty-five years. To a large extent, these changes can be directly or indirectly related to forest management and, more specifically, to recent mechanization of forestry (**H1**), which surpass regional (e.g. increased deer density) and global (e.g. climate warming) forces. These changes only partly differed among soil types, depending upon their susceptibility to soil compaction and their associated habitat species pool (**H2**). They are mostly explained by the non-random, directional colonization of forest plant communities by the same suite of species while very few species went locally extinct at random, causing a general increase in species richness of vascular plant species in the herb layer at both the stand ( $\alpha$ -diversity) and forest ( $\gamma$ -diversity) scales (**H3**), and a homogenisation of species composition among habitats (i.e. decreased  $\beta$ -diversity; **H4**). Not only taxonomic diversity was altered, but also the functional and phylogenetic diversity of the forest herb layer, suggesting that these changes will have long-term effects on forest ecosystem functioning. Below we discuss these main findings, which suggest that the driver of forestry vehicles also drives herb layer changes in managed temperate forests.

## Management practices are the key driver of vegetation changes

The comparison between managed and unmanaged stands on the same soil type (luvisols) enables us to single out the role of forest management (**H1**).

Firstly, in managed stands only, EIV\_L emerged from the CICT analysis as the most important trait explaining vegetation changes over the last 45 years, with an increased frequency of shade-tolerant species. This increase is consistent with the increased importance of shade-casting tree species in the canopy. At the same time, light-demanding species are able to maintain or (re-)establish due to the lack of significant changes in canopy structure (i.e., tree and shrub cover, shade-casting ability index), as a likely consequence of repeated thinning operations which maintain trails across stands. This may explain why forest specialists (forest maturation) and generalists (thinning-associated disturbances) both increased in absolute abundance and why plant communities showed an increased mean EIV\_L despite the increased cover-abundance of shade-tolerant species. Also, due to the time-lag in the response of the forest herb layer to recent canopy changes, the observed vegetation may not reflect current understory light conditions. Consistently, unmanaged stands showed a decreased EIV\_L (and increased LQ) associated with the strong increased cover of shade-casting species in the overstories (i.e. beech, hornbeam and sycamore maple) and the invasive spread of *P. serotina*. Aside from altered light conditions at the forest floor, the increased EIV\_T and EIV\_K in managed stands suggests that forest microclimate cannot buffer understory plant responses to macroclimate warming (De Frenne et al. 2013), in contrast with unmanaged stands.

Secondly, our trait-based approach highlights the importance of management mechanization in driving the observed changes, especially on luvisols which are highly susceptible to soil compaction (Cambi et al. 2015). First, the strong increase in EIV\_F and proportion of anemochores and hydrochores can be related to the deep ruts left by forestry vehicles, that are micro-habitats favourable to a number of species. In the field, the vertical ridge of recent wheel tracks was often covered by thousands of fern prothallus, while older tracks hosted dense (linear) populations of

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mature ferns. Ferns are well-known as wind-dispersed species requiring bare soil conditions for optimal development of prothallus (Flinn & Marks 2007). Similarly, temporary micro-ponds into ruts benefit to hygrophilous graminoids (sedges, rushes and grasses). More generally, skid trails act as corridors for a number of shade-tolerant hygrophilous species, eventually coming from adjacent open habitats, to spread throughout managed stands (Buckley et al. 2003, Avon et al. 2013, Wei et al. 2016). Increased cover-abundance of ferns and graminoids have been repeatedly observed in managed high forest systems (Decocq et al. 2004, Baeten et al. 2009, Müllerová, Hédli & Szabó 2015, Heinrichs & Schmidt 2017). Most of these species are also known as agestochoric species (i.e., species dispersed by forestry vehicles; Bossuyt, Heyn & Hermy 2002, Decocq et al. 2004). The pervasiveness of skid trails in high forest systems (Avon et al 2013), combined with the huge amount of diaspore-containing mud carried by forestry vehicles likely makes this non-conventional mean of dispersal of utmost importance in managed forests and contributes to compositional changes. Second, the increased frequency/abundance of nitrogen-demanding species in managed stands cannot be explained by the increased cover of high litter quality, shade-tolerant species in overstories (Verheyen et al. 2012), which predominated in reserves. Nor can it be explained by global atmospheric N deposition alone, since the two reserves surrounded by managed stands were far less affected. However, since canopy openness is higher in managed than in unmanaged stands, N mineralization is likely greater in the former (De Frenne et al. 2013). More likely, we suspect an effect of local N deposition due to pollutants emitted from forestry vehicle exhausts and engine degradation. Several roadside studies revealed a strong decreasing gradient of N deposition within 50-100m away from roads, which paralleled a decline of EIV\_N and intensity of plant compositional changes (Bignal et al. 2007, Lee & Power 2013). We expect similar effects in managed forests, especially below canopies where the low air circulation likely reduces gas velocity.

Surprisingly, we found no significant effect of the recent increase in deer density, as indicated by the unchanged EIV\_BA and decreased proportion of endozoochorous species. This may be because we resurveyed only closed-canopy stands while deers preferentially forage inside

clearings, young tree plantations and along lanes (Kuijper et al. 2009 and references therein). Also, the increased resource availability (cf. local nitrogen deposits combined with thinning-induced light pulses; De Frenne et al. 2013) may compensate over deer pressure by disproportionately increasing the cover-abundance of nitrogen-demanding species (Bernhardt-Römermann et al. 2015).

### **Vegetation changes are (still) soil type-dependent**

The comparison of similarly managed stands across different soil types enables us to single out the role of soil type in the response of vegetation to environmental changes (**H2**). As expected, vegetation changes were primarily explained by traits responding to canopy openness (i.e. EIV\_L), with the notable exception of podzols.

Due to their high productivity, luvisols are more intensively managed than stands on other soil types and thus showed the highest changes in community weighted mean trait values (see above). Consistently, luvisols experienced a strong increase of EIV\_N, EIV\_F and CSI; and the strongest shift of CSR signature towards R-strategists.

In comparison, cambisols underwent less pronounced changes though they are also quite intensively managed, suggesting a higher resilience to management-associated disturbances, especially to soil compaction (Cambi et al. 2015).

The decreased EIV\_L but increased EIV\_N observed on podzols are consistent with the spread of shade-casting tree species (i.e. beech, sycamore maple and hornbeam) and of the invasive *P. serotina*. This spread likely creates microclimatic conditions that are favourable to tree regeneration, explaining that maximal height was the most discriminant trait of winners according to the CICT analysis. Moreover, these conditions may mitigate the effect of global warming (De Frenne et al. 2013), hence the lack of vegetation thermophilization. Except beech, all these species have a litter with a high N content, which may be responsible for the increased EIV\_BA.

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Glaysols were characterized by a spectacular spread of shade-tolerant species at the expense of light-demanding species. The decrease in EIV\_L and K suggests canopy closure since 1970, although the tree cover was lower in 2015 than in 1970, due to the recent dieback of the canopy-dominant ash. This indicates a time lag in the response of the herb layer and that a future shift towards more light-demanding species is likely.

### **Non-random compositional changes impact community diversity**

As expected, managed stands underwent an increase in taxonomic, functional and phylogenetic diversity (**H3**), but to a lesser degree, this increase was also observed in unmanaged stands. Despite no major change in management since 1970, community richness and diversity increased at the stand scale ( $\alpha$ -diversity), predominantly in managed stands and irrespective of the soil type considered. This contrasts with the few other resurveys that evidenced an increased species richness, which dealt with fragmented forests (e.g. Naaf & Wulf 2010, Naaf & Kolk 2016), forests released from a major disturbance (e.g. fire suppression in McCune & Vellend 2013, Li & Waller 2015; recent management cessation in Vanhellefont et al. 2014, Reczynska & Swierkosz 2017), or forests recently submitted to a new disturbance (e.g. deer browsing in Vild et al. 2017). These taxonomic changes were associated with changes in functional and phylogenetic diversities, but for managed stands, once the effect of species richness removed, they usually remained unchanged (see *FEve*, *RaoQ*, *PSE*, *PSV*) or even decreased (*PSE* and *PSV* on cambisols). Compared to the other soil types, podzols gained less species, but those introduced new traits in the extent community, as revealed by the disproportional increase in functional (*RaoQ*) and phylogenetic (*PD*, *PSR*) diversity. In contrast, in unmanaged stands, both functional and phylogenetic diversities increased independently from species richness (see e.g. *RaoQ*), indicating the increasing co-occurrence of non-related species with contrasted traits. This is a plausible effect of increased environmental heterogeneity within aging stands (e.g. small gaps into closed-canopy patches, treefall-induced microhabitats) (Scheller &

Mladenoff 2002). This is well reflected by the diversity of winner species, which include gap-dependent grasses (e.g. *Calamagrostis epigejos*), forbs (e.g. *Teucrium scorodonia*), undershrubs (e.g. *Rubus idaeus*), and saplings (e.g. *Sorbus aucuparia*), as well as late-successional shade avoiders (e.g. *Anemone nemorosa*) and shade-tolerant forbs (e.g. *Viola reichenbachiana*), ferns (e.g. *Athyrium filix-femina*) and sedges (e.g. *Carex sylvatica*).

Consistently, compositional homogenization applied not only to managed stands (**H4**), but also to unmanaged stands. Despite the overall homogenization of the forest herb layer, the intensity of changes in managed stands depended upon initial site conditions (Bunn et al. 2010, Naaf & Kolk 2016), with the species gain roughly proportional to the initial (1970) species richness and the size of the corresponding habitat species-pool.

The same suite of winners was retrieved across managed stands, explaining why spatial  $\beta$ -diversity decreased, a pattern retrieved by all legacy studies in forests, be the latter managed or not (Durak & Holeska 2015, Savage & Vellend 2015, Heinrichs & Schmidt 2017). This also explains why temporal  $\beta$ -diversity was composed, to a large extent, of nestedness (i.e. communities recorded in 1970 were primarily subsets of those observed in 2015). Winner species were mostly ferns, tree saplings, shade-avoiders (i.e. vernal geophytes) and shade-tolerant species, whose increased frequency has been observed throughout European temperate forests (Verheyen et al. 2012, Bernhardt-Römermann et al. 2015). In contrast with former legacy studies, this reduced  $\beta$ -diversity was not due to the spread of exotic species (Rooney et al. 2004, Rogers et al. 2008) and occurred alongside increased  $\alpha$ -diversity (Naaf & Wulf 2010, Li & Waller 2015). The colonization of stands by the same suite of disturbance-tolerant (cf. shift of the CSR signature towards R-strategists), generalist species clearly contributes to the homogenization (Clavel, Julliard & Devictor 2010, McCune & Vellend 2013). Moreover, like in other resurveys (e.g. Verheyen et al. 2012, Jantsch et al. 2013, Vanhellefont et al. 2014), winners included tree and shrub saplings. This has been attributed to more frequent mast years and increased seedling performance and survival due to climate warming

and soil eutrophication (Övergaard, Gemmel & Karlsson 2007, Callahan et al. 2008, Smaill et al. 2011).

On the other hand, we found few losers, hence the low importance of the turnover component of temporal  $\beta$ -diversity. Loser species differed among soil types and from one plot to another, and were always rare in 1970, suggesting rather local extinction (i.e., rare species have a higher probability to be extirpated) than pseudo-extinction (i.e., due to the relocation/observer error). At the entire forest scale,  $\beta$ -diversity thus decreased, while species richness ( $\gamma$ -diversity) increased, because non-random (i.e. trait-determined) colonization events surpassed random extinction processes (i.e. independent from species traits). At the same time, colonizers likely introduced novel traits and phyla in extent local communities, as revealed by the disproportionate importance of nestedness over turnover underlying phylogenetic and functional homogenisation.

### **Concluding remarks**

Previous resurvey studies examining drivers of local changes in the forest herb layer mostly focused on global and/or regional factors, or addressed local factors via changes in forest management. Moreover, they often ignored biases associated with multi-sites comparison, relocation error and inter-observer differences. To our knowledge, our study is the first to minimize these biases while using a trait-based approach to assess the concomitant effect of many drivers nested at multiple scales. We show that even in a forest which has been continuously managed as regular high forest, major changes in species composition and diversity have happened over a relatively short time scale (45 years). The repeated passing of increasingly heavy forestry vehicles across forests stands emerged as the main driver of observed vegetation changes, by directly (diaspore dispersal by vehicles) and indirectly (alteration of understory microclimate and light availability, soil disturbance, local N deposits) impacting plant species composition and diversity. The non-random colonization of forest stands by the same suite of species increased species richness at

both stand ( $\alpha$ -diversity) and forest ( $\gamma$ -diversity) scales but, at the same time, caused compositional homogenisation among habitats (i.e. decreased  $\beta$ -diversity).

We further show for the first time that changes were not only taxonomic, but also functional and phylogenetic, suggesting long-term effects on ecosystem functioning. Although high functional and phylogenetic diversities within communities are expected to enable their rapid adaptation to changing environmental conditions over time (Winter et al. 2009), at the entire forest scale however, functional and phylogenetic homogenization may synchronize responses across local communities and thus threaten functioning, stability and resilience of the forest as a whole (Olden et al. 2004, Winter et al. 2009).

Overall, the patterns of vegetation change we observed are consistent with those reported elsewhere in Europe and, to some extent, in north America, indicating the generality of these patterns in managed temperate forests. The exact ecological role and net effect of management-induced vegetation changes on ecosystem functioning are still uncertain and require further investigation, but they do deserve attention from forest managers and conservationists.

#### **Author's contributions**

DCK and GD conceived the ideas, designed methodology and conducted the field resurvey. TH, DCK and GD analysed the data. DCK and GD led the writing of the manuscript. All co-authors contributed critically to the drafts and gave final approval for publication.

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#### **Data accessibility**

Vegetation plots are deposited in the forestREplot database: <http://www.forestreplot.ugent.be>.

Plant traits data can be retrieved from the LEDA database: <https://www.uni-oldenburg.de/en/landeco/research/leda/data-files> (Kleyer et al., 2008).

#### **References**

Anderson, M.J., Ellingsen, K.E., & McArdle, B.H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683–693.

Anderson, M.J., & Walsh, D.C. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological monographs*, 83, 557-574.

Avon, C., Dumas, Y., & Berges, L. (2013). Management practices increase the impact of roads on plant communities in forests. *Biological Conservation* 159, 24-31.

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, 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.

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 & Conservation*, 21: 1399-1409.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143.

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21(12), 1223-1232.

Baselga, A., & Orme, C.D.L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808-812.

Bernhardt-Romermann, M., Baeten, L., Craven, D., De Frenne, P., Hedl, R., Lenoir, J., ... Verheyen, K. (2015). Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology*, 21(10), 3726–3737.

Accepted Article

Bignal, K.L., M.R. Ashmore, A.D. Headley, K. Stewart & K. Weigert. (2007). Ecological impacts of air pollution from road transport on local vegetation. *Appl. Geochemistry* 22, 1265–1271.

Bossuyt, B., M. Heyn, & M. Hermy. (2002). Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecology* 162, 33-48.

Buckley, D.S., Crow, T.R., Nauertz, E.A., & Schulz, K.E. (2003). Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan USA. *Forest Ecology and Management* 175, 509-520.

Bunn, W.A., Jenkins, A., Claire, B.B., & Sanders N.J. (2010). Change within and among forest communities: the influence of historic disturbance, environmental gradients, and community attributes. *Ecography* 33, 425-434.

Callahan, H.S., Maughan, H., & Steiner, U.K. (2008). Phenotypic plasticity, costs of phenotypes, and costs of plasticity. *The Annals of the New York Academy of Sciences*, 1133, 44–66.

Cambi, M., Certini, G., Neri, F., & Marchi E. (2015). The impact of heavy traffic on forest soils: A review *Forest Ecology and Management*, 338, 124–138.

Clavel J., Julliard R., & Devictor V. (2010). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., & Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics*, 35, 113–147.

De Caceres, M.D. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ... Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46), 18561–18565.

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., Foucault, B., Delelis-Dusollier A., & Bardat, J. (2004). Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. *Journal of Applied Ecology* 41, 1065-1079

Diekmann, M., Brunet, J., Rühling, Å., & Falkengren-Grerup, U. (1999). Effects of nitrogen deposition: results of a temporal-spatial analysis of deciduous forests in South Sweden. *Plant Biology*, 1, 471-481

Durak, T., & Holeksa, J. (2015). Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of managed beech stands. *Forest Ecology and Management*, 351, 47–56.

Ellenberg, H. (1988). Eutrophierung - Veränderung der Waldvegetation - Folgen für den Reh-Wildverbiss und dessen Rückwirkungen auf die Vegetation. *Schweizerische Zeitschrift für Forstwesen*, 139, 261-282.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. & Werner, W. (2001). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 1-262.

Flinn, K.M., Marks, P.L. (2007). Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications* 17, 452–463.

Heinrichs, S., & Schmidt, W. (2017) Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. *Applied Vegetation Science* 20, 271–281.

Helm N.F.E., Mirtl M., & Dirnböck T. (2017). Multiple environmental changes drive forest floor vegetation in a temperate mountain forest. *Ecology and evolution*, 7 (7) 2155–2168.

Helmus, M. R., Bland, T. J., Williams, C. K. & Ives, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist* 169, E68–E83.

Hermy, M. (1985) *Ecologie en fytosociologie van oude en jonge bossen in Binnen-Vlaanderen* (in Dutch). PhD thesis, University of Ghent

Hothorn, T., Hornik, K., & Zeileis, A. (2006). “Unbiased Recursive Partitioning: A Conditional Inference Framework.” *Journal of Computational and Graphical Statistics*, 15(3), 651–674.

Hunt R., Hodgson J.G., Thompson K., Bungener P., Dunnett N.P., Askew A.P.,

Bakker J.P. (2004). A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science* 7(2): 163-170.

Jamoneau, A., Sonnier, G., Chabrierie, O., Closset-Kopp, D., Saguez, R., Gallet-Moron, E., & Decocq G. (2011). Drivers of plant species assemblages in forest patches among contrasted dynamic agricultural landscapes. *Journal of Ecology*, 99, 1152–1161

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

Accepted Article

Jauni, M. & Ramula, S. (2015). Meta-analysis on the effects of exotic plants on the fitness of native plants. *Perspectives in Plant Ecology, Evolution and Systematics*. 17 (5) 412-420

Kapfer, J., Hedl, R., Jurasinski, G., Kopecky, M., Schei, F. H., & Grytnes, J. A. (2017). Resurveying historical vegetation data – opportunities and challenges. *Applied Vegetation Science*, 20(2), 164–171.

Keith, S., Newton, A.C., Morecroft, M.D., Bealey, C.E. & Bullock, J.M. (2009). Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society, Series B: Biological Sciences* 276: 3539–3544

Kleyer M., Bekker R. M., Knevel I. C., Bakker J. P., Thompson K., Sonnenschein M., Poschlod P., van Groenendael J. M., Klimeš L., Klimešová J., Klotz S., Rusch G. M., Hermy M., Adriaens D., Boedeltje G., Bossuyt B., Endels P., Götzenberger L., Hodgson J. G., Jackel A.-K., Dannemann A., Kühn I., Kunzmann D., Ozinga W. A., Römermann C., Stadler M., Schlegelmilch J., Steendam H. J., Tackenberg O., Wilmann B., Cornelissen J. H. C., Eriksson O., Garnier E., Fitter A. & Peco B. (2008): The LEDA Traitbase: a database of life-history traits of the Northwest European flora. – *J. Ecol.* 96: 1266–1274.

Kopecký, M., & Macek, M. (2015). Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, 21(3), 322–330.

Kuijper, D.P.J., Cromsigt, J.P.M.G., Churski, M., Adams, B., Jedrzejewska, B., & Jedrzejewski, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forests? *Forest Ecology and Management*, 258, 1528–1535.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91 (1) 299-305.

Lambinon J., De Langhe J.E., Delvosalle L., Duvigneaud J. (1992). *Nouvelle Flore de la Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des Régions voisines. Références : Editions du patrimoine du Jardin botanique national de Belgique*, 1092 p.

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.

Lee, M.A. & Power, S.A. (2013). Direct and indirect effects of roads and road vehicles on the plant community composition of calcareous grasslands. *Environmental Pollution*, 176, 106-113.

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P.F., Belwood, D.R., & Mouillot, D. (2012). Quantifying phylogenetic beta diversity: distinguishing between "true" turnover of lineages and phylogenetic diversity gradients. *PLoS One* 7(8): e42760.



Li, D., & Waller, D. (2015). Drivers of observed biotic homogenization in pine barrens of central Wisconsin. *Ecology* 96, 1030–1041.

McCune J. L., & Vellend M. (2013). Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. *Journal of Ecology*, 101, 1542–1551.

Morrison, L.W. (2016). Observer error in vegetation surveys: a review. *Journal of plant Ecology*, 9 (4), 367-379.

Mouchet, M.A., Villéger, S., Mason, N.W.H., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876

Müllerová, J., Hédli, R., & Szabó, P. (2015). Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management*, 343, 88–100

Naaf, T., Kolk, J. (2016). Initial site conditions and interactions between multiple drivers determine herb-layer changes over five decades in temperate forests. *Forest Ecology and Management*, 366, 153–165

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

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. (2012). *vegan*: Community ecology package: R package version 2.1-13/r2115.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, 19, 18-24

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.

Pearse, W.D., Cadotte, M.W., Cavender-Bares, J., Ives, A.R., Tucker, C.M., Walker, S.C. & Helmus, M.R. (2015). *pez*: phylogenetics for the environmental sciences. *Bioinformatics*, 31: 2888–2890.

R Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reczynska, K., & Swierkosz, K. (2017). Compositional changes in thermophilous oak forests in Poland over time: do they correspond to European trends? *Applied Vegetation Science* 20, 293–303

Rogers, D., Rooney, T.P., Olson, D., & Waller, D.M. (2008). Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. *Ecology*, 89, 2482–92

Rooney, T.P., Wiegmann, S.M., Rogers, D., & Waller, D.M. (2004). Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, 18, 787–798

Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 38, 546–555

Scheller, R.M., & Mladenoff, D.J. (2002). Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecological Application*, 12, 1329-1343

Smaill, S.J., Clinton, P.W., Allen, R.B., & Davis, M.R. (2011). Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, 99 (3) 870-877

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. & Firbank, L.G. (2006). Biotic homogenization and changes in species diversity 15 across human-modified ecosystems. *Proceedings of the Royal Society of London. Series B*, 263, 2659-2665.

Tombal, P. (1972) Recherche sur les potentialités phytocoenologiques de la forêt de Compiègne (Oise, France). *Bulletin de la Société Botanique du Nord de la France* 25, 31 - 52

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, O., ... Decocq, G. (2015) The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Global Ecology and Biogeography* 24, 1094–1105.

Van Calster, H., Baeten, L., De Schrijver, A., De Keersmaeker, 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

Van der Maarel, E. (1979). Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39, 97–114

Vanhellemont, M. (2014). Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. *Plant Ecology and Evolution*, 147, 22–32

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Verstraeten, G. (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, 100, 352–365

Accepted Article

Verheyen, K., De Frenne, P., Baeten, L., Waller, D., Hedl, R., Perring, M., ....Bernhardt-Romermann, M. (2017). Combining community resurvey data to advance global change research. *BioScience*, 67, 73-83

Vild, O., Kopeck, R., Szab, Y.M.O., & Zouhar, P.S. (2017). The paradox of long-term ungulate impact: increase of plant species richness in a temperate forest. *Applied Vegetation Science*, 20(2), 282-292.

Villéger, S. Grenouillet, G., & Brosse, S. (2013). Decomposing functional beta-diversity reveals that low functional beta-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, 22, 671-681

Villéger S., Novack-Gottshal P. & Mouillot D. (2011). The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters*. 14, 561–568

Wei, L., F. Hulin, R.F. Chevalier, F. Archaux, and F. Gosselin. (2016). Is plant diversity on tractor trails more influenced by disturbance than by soil characteristics? *Forest Ecology and Management* 379: 173-184.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and soil*, 199, 213-227

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M, ....Kuhn I. (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences. USA*, 106, 21721–21725.

### **Tables and Figures**

Table 1. Hypothesized drivers and processes behind vegetation changes and predicted changes of proxies across soil and management types.

Table 2. Overstory changes between 1970 and 2015.

Table 3. Changes in community weighted means (CWM) of the different species traits between 1970 and 2015 (using MAX matrices).

Table 4. Diversity changes within the forest herb layer between 1970 and 2015 (using MAX matrices).

Fig. 1. Conditional inference classification and regression trees highlighting the most discriminant traits explaining compositional changes between 1970 and 2015 (using MAX matrices). L and F are Ellenberg indicator values for light and soil moisture, respectively.

Fig. 2. Diagrams defined by the first two axes of a principal coordinates analysis (PCoA) run on the species\*relevés matrices of the entire forest (a), unmanaged stands on luvisols (b), and managed stands on luvisols (c), podzols (d), cambisols (e) and gleysols (f). Panels b to f thus represent subsets of panel a. Each plot is shown by a point and labelled by the survey year (hence, two points per plot). Results of tests for community compositional shift (PERMANOVA test) and homogenization (PERMDISP test) between 1970 and 2015 (using MAX matrices) are reported on each panel.

Fig. 3. Partitioning of the compositional, functional and phylogenetic dissimilarity between 1970 and 2015 into turnover and nestedness components, based on MAX matrices.

### Supporting information

**Appendix S1.** Extended information on the calculation of functional and phylogenetic diversity indices.

**Table S1.** Changes in  $\gamma$ diversity (species richness and composition) between 1970 and 2015 (using MAX and MIN matrices).

**Table S2.** Changes in community weighted means (CWM) of the different species traits between 1970 and 2015 (using MIN matrices).

**Table S3.** Diversity changes within the forest herb layer between 1970 and 2015 (using MIN matrices).

**Fig. S1.** Conditional inference classification and regression trees highlighting the most discriminant traits explaining compositional changes between 1970 and 2015 (using MIN matrices).

**Fig. S1.** Diagrams defined by the first two axes of a principal coordinates analysis (PCoA) run on the community compositional (**A**; MIN matrices), functional (**B**; MAX and MIN matrices) and phylogenetic (**C**; MAX and MIN matrices) matrices of the entire forest (a), unmanaged stands on luvisols (b), and managed stands on luvisols (c), podzols (d), cambisols (e) and gleysols (f). Panels b to f thus represent subsets of panel a. Each plot is shown by a point and labelled by the survey year (hence, two points per plot). Results of tests for community compositional shift (PERMANOVA test) and homogenization (PERMDISP test) between 1970 and 2015 using MAX matrices are reported on each panel.

**Fig. S3.** Partitioning of the compositional, functional and phylogenetic dissimilarity between 1970 and 2015 into turnover and nestedness components (MIN matrices).



**Table 1**

Scale	Driver	Process	Proxies	Predicted change	Management effect	Soil effect
Global	Climate warming	Increased mean temperature in the understoreys promotes warm-adapted species at the expense of cold-adapted species	EIV_T	increase	M+>M0	P>L,G>C
Regional	Atmospheric N deposits	Soil eutrophication promotes nitrogen-demanding, ruderal generalists at the expense of oligotrophic, specialist species; soil acidification promotes acidophilous species	EIV_N	increase	M+>M0	P>L>C,G
			CSR signature	shift towards R-strategists		
			CSI	increase		
			EIV_R	decrease		
Regional	Increased ungulate density	Overbrowsing on palatable plants which then decrease in abundance	EIV_BA	decrease	M+>M0	
		Increased dispersal of diaspores attaching fur or eaten by deers	Epi- and endozoochory	increased abundance		
Local	Increased overstorey density	Canopy closure induced by the increased abundance of common beech (natural succession) and/or <i>Prunus serotina</i> (invasion) reduces light availability and buffers against warming and climatic fluctuations, but increases the amount of litter and air humidity at the forest floor	R%T, R%S, R%TS, SCA	increase	M0>M+	P>L>G>C
			LQ, EIV_N	decrease (beech) or increase ( <i>Prunus serotina</i> )		
			EIV_L, EIV_K, EIV_T	decrease		
			CSR signature	shift towards S-strategists		
			CSI	decrease		
Local	Silviculture mechanization	The repeated passing of forestry vehicles induces soil compaction and baring, and imports diaspores from non-forest habitats	EIV_F	increase	M+>M0	L,G>C>P
			hydrochory	increased abundance		
			CSR signature	shift towards R-strategists		
			CSI	increase		

**Proxies:** EIV: Ellenberg indicator value for light (L), temperature (T), continentality (K), soil reaction (R), soil nutrient (N) and browsing attractiveness (BA); CSI: community specialization index; R%: cover of tree layer (T), shrub layer (S), both tree and shrub layers (TS); SCA: shade casting ability of canopy trees; LQ: litter quality of canopy trees. **Management type:** M+: managed stands, M0: unmanaged stands. **Soil types:** L: luvisols, P: podzols, C: cambisols, G: gleysols.

Table 2

Management		Years	All stands	Reserve	Managed			
Soil type			All stands	Luvisols	Luvisols	Podzols	Cambisols	Gleysols
Canopy cover	R%T	1970	74.83±2.48	55.18±7.11	83.7±3.6	69.64±6.68	76.25±5.05	79.62±4.37
		2015	72.89±1.52	80.91±2.11	77.39±2.2	70±4.19	72.67±2.06	61.54±4.51
			NS	***	NS	NS	NS	*
	R%S	1970	36.01±3.64	78.64±3.88	15.52±5.13	39.07±7.05	29.5±7.56	40.92±7.55
		2015	37.34±2.53	59.09±5.63	26.52±3.86	37.50±5.31	33.12±5.22	43.08±6.34
			NS	*	*	NS	NS	NS
	R%TS	1970	110.84±3.65	133.82±8.18	99.22±5.41	108.71±6.02	105.75±9.49	120.54±10.43
		2015	109.29±2.9	140.00±5.56	103.91±3.37	107.5±5.85	101.25±7.85	104.62±6.47
			NS	NS	NS	NS	NS	NS
	R%H	1970	52.6±3.95	25.36±9.49	48.52±7.58	53.86±9.24	56.31±8.12	76.92±5.48
		2015	65.32±2.69	37.27±5.06	70.87±3.66	66.07±6.55	62.19±6.66	82.31±2.57
			***	NS	**	NS	NS	NS
Canopy traits (CWM)	LQ	1970	2.08±0.12	1.52±0.08	1.88±0.15	1.54±0.11	1.83±0.26	3.8±0.17
		2015	2.23±0.08	2.0±0.05	2.05±0.11	1.75±0.11	2.09±0.17	3.41±0.1
			*	***	NS	*	NS	*
	SCA	1970	3.87±0.12	4.01±0.14	4.37±0.12	2.91±0.41	4.54±0.15	3.08±0.09
		2015	3.92±0.08	4.06±0.08	4.20±0.09	3.53±0.27	4.35±0.10	3.21±0.13
			NS	NS	NS	**	NS	NS
Tree species contribution	Fagus	1970	4.94	5.82	6.65	3.64	6.58	
		2015	6.28	7.91	7.65	5.79	7.65	
			***	**	*	**	*	
	Pavium	1970	0.05		0.18		0	
		2015	0.34		0.64		0.47	
			**		*	*		
	Acer	1970	0.46	0	1.23	0.14		
		2015	1.74	4.00	2.88	0.71		
			***	**	*	NS		
	Carpinus	1970	1.77	0.45	0.82	0.57		
		2015	2.85	2.45	1.94	2.07		
			***	**	*	*		
	Ulmus	1970	0.44					2.61
		2015	0.08					0.46
			*					*
	Ilex	1970	0.04					
		2015	0.19					
			NS					
	Pserotina	1970	0.06	0.45		0		
		2015	0.83	2.00		1.57		
			***	*		*		

R%: estimated cover of the tree (T), shrub (S), tree+shrub (TS) and herb (H) layers in %. CWM: community weighted means for litter quality (LQ) and shade-casting ability (SCA). Tree species contribution of *Fagus sylvatica* (Fagus), *Prunus avium* (Pavium), *Acer pseudoplatanus* (Acer), *Carpinus betulus* (Carpinus), *Ulmus minor* (Ulmus), *Ilex aquifolium* (Ilex) and *Prunus serotina* (Pserotina) are expressed as averaged cover-abundance scores on the van der Maarel (1979) scale. Significance of paired *t*-tests between 1970 and 2015 values: NS:  $P > 0.05$ , \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$ .

**Table 3**

Management	Years	All stands	Reserve					Managed			
			All soil types	Luvissols	Luvissols	Podzols	Cambisols	Gleysols			
EIV_L	1970	4.71±0.11	4.95±0.12	3.74±0.1	5.68±0.12	4.29±0.21	5.66±0.2				
	2015	4.65±0.06	4.65±0.07	4.34±0.1	5.1±0.15	4.29±0.08	5.17±0.12				
		NS	*	***	***	NS	*				
EIV_F	1970	5.37±0.06	5.24±0.07	5.23±0.05	5.13±0.12	5.22±0.06	6.18±0.14				
	2015	5.59±0.05	5.37±0.04	5.47±0.04	5.45±0.08	5.44±0.05	6.31±0.1				
		***	NS	***	*	***	NS				
EIV_R	1970	5.56±0.13	4.99±0.23	5.60±0.09	3.91±0.21	6.36±0.13	6.74±0.07				
	2015	5.68±0.08	5.18±0.08	5.79±0.08	4.71±0.19	6.20±0.06	6.33±0.09				
		NS	NS	*	***	NS	***				
EIV_N	1970	5.13±0.10	4.89±0.22	5.38±0.07	3.84±0.16	5.40±0.16	5.95±0.16				
	2015	5.45±0.06	5.25±0.07	5.59±0.06	4.65±0.15	5.77±0.11	5.86±0.08				
		***	NS	**	***	**	NS				
EIV_T	1970	5.24±0.03	5.20±0.07	5.15±0.04	5.23±0.1	5.32±0.06	5.33±0.05				
	2015	5.3±0.01	5.38±0.04	5.26±0.03	5.33±0.04	5.28±0.02	5.29±0.02				
		*	NS	***	NS	NS	NS				
EIV_K	1970	2.96±0.04	2.76±0.1	2.78±0.06	2.95±0.08	2.98±0.07	3.42±0.08				
	2015	3.07±0.02	2.9±0.03	3.08±0.03	2.97±0.05	3.13±0.03	3.23±0.03				
		**	NS	***	NS	NS	*				
EIV_BA	1970	2.74±0.07	2.64±0.22	2.91±0.11	2.27±0.12	2.61±0.09	3.17±0.13				
	2015	2.95±0.03	3.06±0.07	2.97±0.04	2.79±0.07	2.95±0.04	3.01±0.07				
		**	NS	NS	**	**	NS				
CSR signature_C	1970	0.47±0.12	0.60±0.11	0.38±0.05	0.53±0.15	0.39±0.08	0.55±0.06				
	2015	0.46±0.06	0.53±0.06	0.40±0.03	0.48±0.03	0.43±0.02	0.50±0.05				
		NS	NS	NS	NS	NS	*				
CSR signature_S	1970	0.42±0.10	0.36±0.09	0.48±0.04	0.41±0.12	0.48±0.06	0.32±0.09				
	2015	0.40±0.06	0.40±0.04	0.41±0.04	0.43±0.05	0.43±0.06	0.31±0.03				
		**	NS	***	NS	**	NS				
CSR signature_R	1970	0.10±0.07	0.04±0.06	0.13±0.07	0.07±0.04	0.12±0.06	0.12±0.07				
	2015	0.14±0.06	0.07±0.04	0.19±0.03	0.09±0.04	0.14±0.05	0.18±0.03				
		***	NS	***	*	NS	*				
Epizoochores	1970	0.17±0.14	0.05±0.12	0.20±0.11	0.15±0.14	0.24±0.15	0.13±0.10				
	2015	0.18±0.07	0.11±0.07	0.23±0.05	0.13±0.06	0.22±0.05	0.18±0.03				
		NS	NS	NS	NS	NS	NS				
Endozoochores	1970	0.30±0.19	0.51±0.22	0.30±0.16	0.20±0.14	0.19±0.14	0.36±0.16				
	2015	0.27±0.11	0.43±0.09	0.21±0.06	0.34±0.08	0.23±0.07	0.21±0.05				
		NS	NS	*	**	NS	*				
Anemochores	1970	0.20±0.17	0.31±0.18	0.12±0.09	0.38±0.19	0.17±0.15	0.12±0.07				
	2015	0.24±0.07	0.31±0.08	0.21±0.06	0.29±0.06	0.23±0.07	0.20±0.03				
		**	NS	***	NS	NS	*				
Hydrochores	1970	0.02±0.07	0.00±0.00	0.01±0.02	0.00±0.00	0.00±0.00	0.13±0.11				
	2015	0.03±0.06	0.01±0.01	0.02±0.02	0.01±0.02	0.01±0.01	0.15±0.09				
		***	NS	*	NS	*	NS				
Myrmecochores	1970	0.12±0.12	0.03±0.06	0.17±0.11	0.08±0.12	0.16±0.15	0.09±0.09				
	2015	0.10±0.06	0.06±0.06	0.12±0.06	0.06±0.06	0.15±0.06	0.09±0.03				
		NS	*	NS	NS	NS	NS				
Others	1970	0.19±0.16	0.10±0.12	0.20±0.17	0.19±0.14	0.24±0.23	0.17±0.11				
	2015	0.17±0.07	0.08±0.05	0.21±0.08	0.17±0.05	0.17±0.05	0.17±0.06				
		NS	NS	NS	NS	NS	NS				
CSI	1970	1.72±0.48	1.49±0.33	1.33±0.24	1.89±0.33	1.74±0.42	2.37±0.29				
	2015	1.85±0.25	1.78±0.16	1.70±0.24	1.93±0.23	1.81±0.14	2.16±0.15				
		**	*	***	NS	NS	*				

All quantitative traits are expressed as community weighted means (CWM) and tested for difference between 1970 and 2015 using paired t-tests. EIV: Ellenberg indicator values for light (L), soil moisture (F), soil reaction (R), soil nutrient (N), temperature (T), continentality (K) and browsing attractiveness (BA); SLA: specific leaf area; CSI: community specialization index.

Qualitative traits were treated as proportional weighted means per category of trait and tested for difference between 1970 and 2015 using paired Wilcoxon rank tests.

All values are means ± 1SD. NS:  $P > 0.05$ , \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$ ; shaded cells indicate that the significance/non significance is not achieved when using the MIN matrix (see Table S2).

**Table 4**

Management	Soil type	Years	All stands		Reserve	Managed			
			All stands	Luvisols	Luvisols	Podzols	Cambisols	Glaysols	
Taxonomic diversity	S	1970	10.77±0.73	7.09±1.38	12.83±1.62	7.57±1.17	9.44±1.08	15.31±1.46	
		2015	34.78±1.35	22.09±2.21	38.09±2.04	24.64±1.32	40.62±2.60	43.38±2.66	
			***	***	***	***	***	***	
	D	1970	0.83±0.01	0.77±0.04	0.85±0.02	0.76±0.04	0.83±0.03	0.91±0.01	
		2015	0.96±0.00	0.93±0.01	0.96±0.00	0.95±0.00	0.97±0.00	0.97±0.00	
			***	***	***	***	***	***	
	H'	1970	2.08±0.07	1.71±0.18	2.24±0.13	1.74±0.18	2.02±0.14	2.56±0.10	
		2015	3.35±0.04	2.91±0.12	3.47±0.06	3.06±0.05	3.53±0.07	3.62±0.06	
			***	**	***	**	**	***	
	J'	1970	0.94±0.01	0.95±0.02	0.93±0.01	0.93±0.02	0.95±0.01	0.96±0.00	
		2015	0.96±0.00	0.96±0.00	0.96±0.00	0.96±0.00	0.96±0.00	0.97±0.00	
			***	NS	NS	NS	NS	NS	
Functional diversity	FRic	1970	5.17±0.52	3.44±1.36	4.49±0.55	5.24±1.62	6.46±1.29	5.98±1.49	
		2015	17.12±1.52	14.28±2.27	17.21±3.09	17.52±3.86	20.34±3.53	15.00±3.62	
			***	***	***	**	**	*	
	FEve	1970	0.54±0.02	0.58±0.07	0.53±0.03	0.52±0.07	0.53±0.03	0.54±0.04	
		2015	0.49±0.01	0.57±0.02	0.47±0.01	0.54±0.01	0.46±0.02	0.45±0.03	
			*	NS	NS	NS	NS	NS	
	FDiv	1970	0.73±0.01	0.74±0.03	0.74±0.02	0.72±0.02	0.70±0.02	0.73±0.02	
		2015	0.76±0.00	0.76±0.02	0.76±0.01	0.74±0.01	0.75±0.01	0.76±0.01	
			**	NS	NS	NS	NS	NS	
	RaoQ	1970	3.02±0.24	2.92±0.66	3.44±0.25	2.46±0.73	3.24±0.67	2.71±0.49	
		2015	4.56±0.26	5.90±0.49	4.06±0.42	5.99±0.74	4.01±0.41	3.42±0.65	
			***	***	NS	**	NS	NS	
Phylogenetic diversity	PD	1970	1461±51	1332±121	1590±96	1273±90	1256±94	1796±125	
		2015	3285±90	2432±151	3421±135	2692±60	3639±180	3972±191	
			***	***	***	***	***	***	
	PSV	1970	0.45±0.02	0.32±0.02	0.51±0.04	0.38±0.03	0.60±0.03	0.35±0.03	
		2015	0.42±0.01	0.41±0.01	0.45±0.01	0.38±0.01	0.45±0.02	0.39±0.01	
			*	**	NS	NS	***	NS	
	PSR	1970	4.30±0.25	4.71±0.75	4.68±0.42	3.59±0.61	3.36±0.29	5.23±0.77	
		2015	14.29±0.49	16.95±1.11	13.75±0.91	15.42±1.10	11.46±0.98	15.23±1.01	
			***	***	***	***	***	***	
	PSE	1970	0.43±0.02	0.31±0.02	0.51±0.03	0.38±0.04	0.55±0.03	0.33±0.02	
		2015	0.43±0.01	0.40±0.01	0.47±0.01	0.37±0.01	0.46±0.02	0.39±0.02	
			NS	**	NS	NS	*	NS	

S: species richness; D: Simpson diversity index; H': Shannon evenness index; J': Pielou equitability index; FRic: functional richness; FEve: functional evenness; FDiv: functional divergence; RaoQ: Rao's quadratic entropy; PD: Faith phylogenetic diversity index; PSV: phylogenetic species variability; PSR: phylogenetic species richness; PSE: phylogenetic species evenness. Values are means ± 1SD. Significance of paired t-tests between 1970 and 2015 values: NS: P>0.05, \*: P<0.05, \*\*: P<0.01, \*\*\*: P<0.001; shaded cells indicate that the significance/non significance is not achieved when using the MIN matrix (see Table S3).

Fig. 1

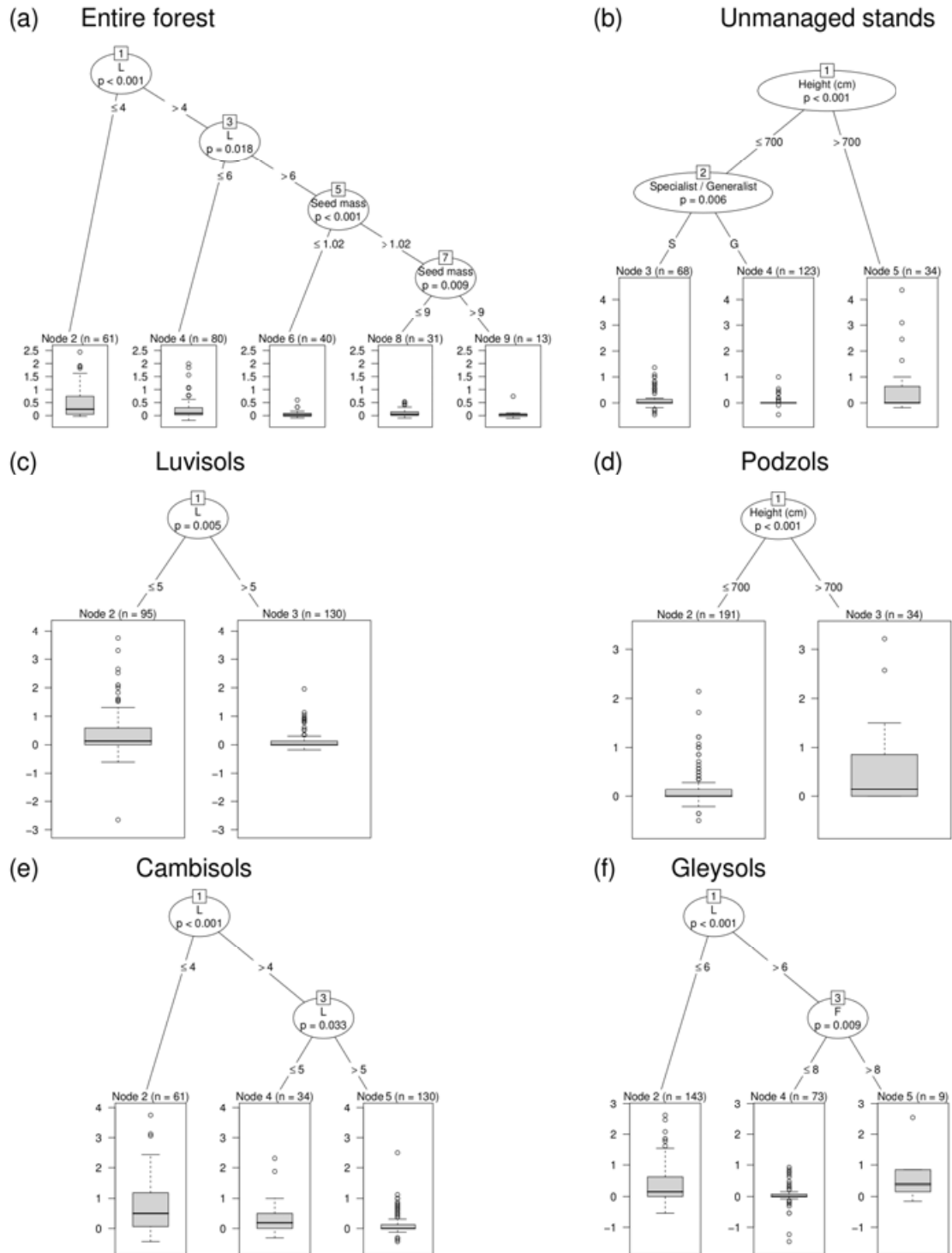


Fig. 2

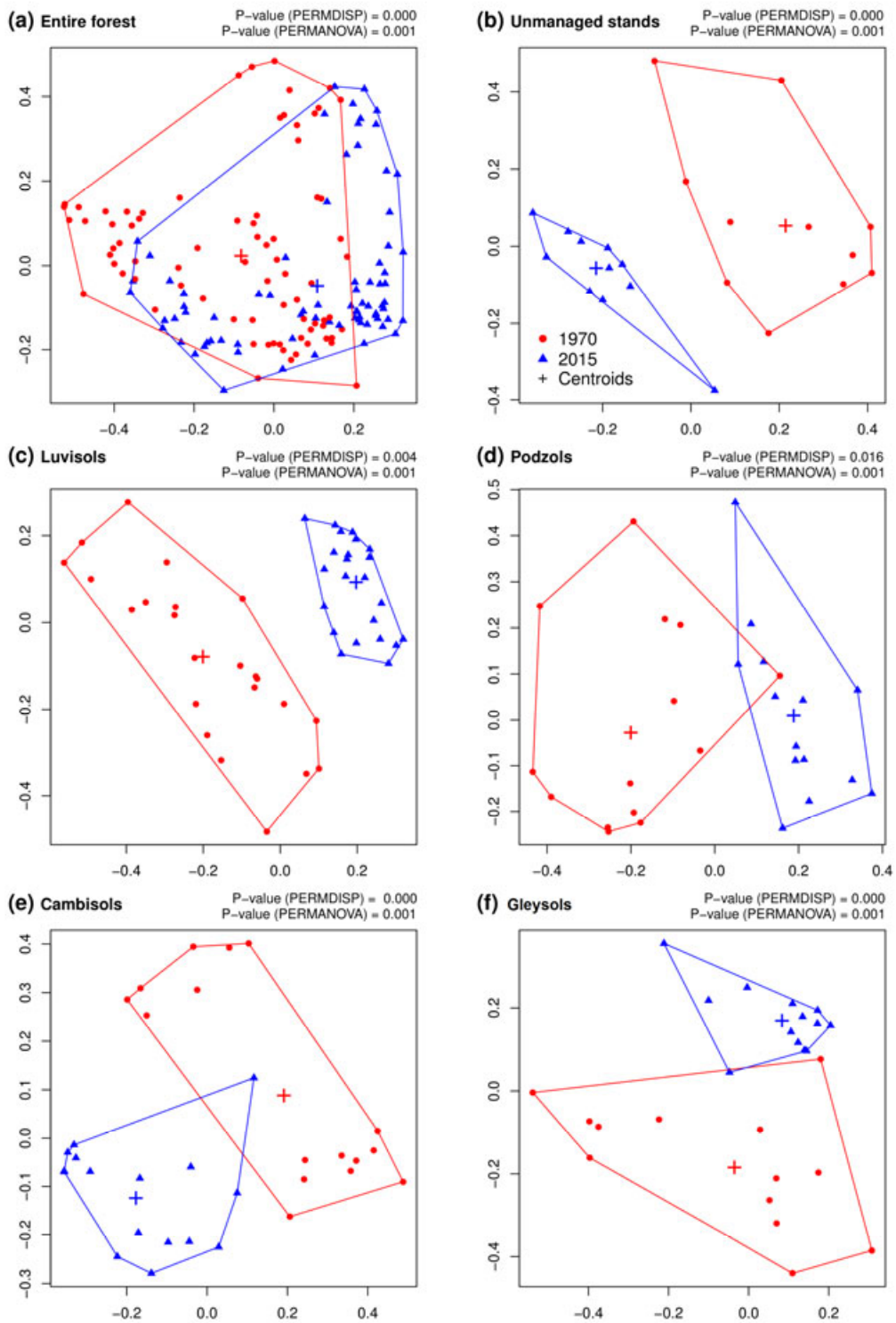


Fig. 3

