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Abstract

Mechanisation is increasingly used in European forest management but so far, few studies have investigated the combined effects of stand attributes and skid trails on stand-scale ground flora diversity. Our study assessed the effects of stand attributes (age, stand type, basal area) and skid trail area on ground flora diversity in 400 m² plots in oak forest stands in the northern half of France. We calculated the richness and abundance of ecological groups based on successional status and light preference. We developed and compared generalized linear models and assessed the magnitude of the effects of each variable. At the ecological group level, floristic variations among plots were mostly associated with stand attributes (stand type or basal area). Although we found non-negligible effects of skid trails on all herbaceous groups, these effects disappeared when tree stand attribute effects were incorporated into the statistical models. At the species level, when incorporating stand attribute effects into the models, skid trail area had weak or inconclusive effects on species (occurrence > 25%) abundance. Since mechanisation is a recent practice in European forests, stronger effects might be expected in the long-term.

Keywords: Ecological group; Stand type; Basal area; Soil compaction; Equivalence tests; Understory diversity

Introduction

Maintaining or improving biodiversity is an important goal of sustainable forest management (Lindenmayer et al. 2000). Ground flora, which is responsible for most floristic diversity in temperate forests (Zenner and Berger 2008), plays multiple important roles in biodiversity (Gilliam 2002). Furthermore, due to its sensitivity to a variety of factors such as overstory characteristics (Augusto et al. 2003; Nagaike et al. 2005; Barbier et al. 2008), soil properties (Bassett et al. 2005; Small and McCarthy 2005), forest disturbances or management practices (Baltzinger et al. 2011; Duguid and Ashton 2013; Wei et al. 2015), ground flora diversity is also an important indicator of forest site quality and of the environmental impact of management (Gilliam 2002).

Many choices made by forest managers influence ground flora. One of the forester's most fundamental acts is the selection of tree species in harvesting and other silvicultural operations. Tree composition and abundance influence micro-environments and resource availability (Barbier et al. 2008; Duguid and Ashton 2013). Indeed, canopy light transmittance can be affected by the properties of tree species such as the spatial arrangement of leaves or leaf size (Kern et al. 2004). Soil water availability is affected by tree species through differing amounts of non-intercepted water or quantity of water absorbed by tree roots (Barbier et al. 2008, 2009). Trees can also greatly influence nutrient cycling by changing the rates of soil organic matter decomposition and nutrient mineralization (Prescott 2002). As a result, changes in tree composition and abundance can impact understory growth and mortality, and modify the competitive interactions among species, especially between shade-tolerant and shade-intolerant species (Baeten et al. 2009). This will in turn induce changes in forest floor species composition and diversity (Barbier et al. 2008). Multiple studies have demonstrated the effects of tree stand characteristics on ground flora diversity. However, these studies provide contrasting or even conflicting results (Augusto et al. 2003;

Barbier et al. 2008). For example, when comparing understory vascular plant diversity in hardwood stands with that in coniferous stands, ten studies showed higher richness under hardwoods, while four studies found the opposite result (Barbier et al. 2008). One reason may be that other potential factors, which may positively or negatively influence the effects of stand attributes on ground flora, have not been identified or disentangled before reaching conclusions (Barbier et al. 2008). Among these factors, management practices can be as important as stand attributes in contributing to inconsistent results (Barbier et al. 2008). Indeed, many practices known to influence ground flora such as how the stand is regenerated, stem density and cutting regime are dependent on the tree species present on the site.

During the last decades, manual felling and logging for forest management has evolved towards mechanized harvesting (Ampoorter et al. 2011). The increasing use of heavier and heavier forestry equipment has the potential to leave durable traces on the soil (typically skid or tractor trails). Skid trails are created by clearing vegetation and crushing forest floor during stand regeneration to provide easy access from roads to stand interiors. They are evenly distributed across the stands; this is especially true in lowland managed forests where management is likely to be intense, as is typical in Europe (Avon et al. 2013). The creation and periodic use of skid trails cause changes in stand structure – for example, by reducing the density of structural legacies (e.g. snags, downed logs, woody debris, uprooted trees, etc.) or opening up the canopy – and stand structure is very important in determining the biodiversity in forests (Rheault et al. 2009). Natural disturbances such as individual (or stand scale) blowdowns and pits and mounds created by uprooting can maintain structural heterogeneity and therefore promote forest biodiversity (Hansen et al. 1991). For this reason, they are considered to be an integral part of natural forest dynamics (Palmer et al. 2000). Unlike these natural disturbances, the disturbances caused by the creation and repeated use of skid trails are more frequent and less varied (Hansen et al. 1991); tracks and trails often become permanent or semi-permanent features in the forest. It is therefore of vital importance that forest managers understand the influence of skid trails on ground flora diversity at the stand scale. Another issue is soil compaction, which causes changes in soil structure (Akbarimehr and Naghdi 2012), reduces porosity (Bassett et al. 2005), increases bulk density (Lotfalian and Bahmani 2011) and water runoff (Akbarimehr and Naghdi 2012) thereby inducing soil erosion (Akbarimehr and Naghdi 2012), and ultimately influences plant regeneration (Bassett et al. 2005) and growth (Lotfalian and Bahmani 2011). The degree of soil compaction is much higher on skid trails than in undisturbed areas in silty soil conditions, and the recovery process may take several decades or even centuries (Godefroid and Koedam 2004). According to Godefroid and Koedam (2004) in their study of a beech forest in central Belgium, the local abundance of 61% of the forest floor species was significantly related to soil compaction. Baltzinger et al. (2011) also indicated that skid trails and tractor ruts may contribute to a significant increase in the floristic diversity at the landscape scale. Hence, skid trails may play an important role in shaping overall ground flora diversity.

The number of skid trails and the total area they cover have typically been chosen as indicators of management or disturbance intensity, especially at large (e.g. landscape) scales (Germain and Munsell 2005; Hosseini et al. 2012). Anderson et al.'s (1976) review showed that the access system (forest roads, skid trails and landings) for forest management ranges from 3 to 30% of the soil area depending on forest type, silvicultural system and topography. Stands of different ages and types within a forest will have different management regimes, and will therefore be subjected to varying intensities of machinery use and different distribution patterns of skid trails (Zenner and Berger 2008). For this reason, it is important to study the effects of skid trails not only at large (e.g. landscape) scales but also at the stand scale.

Our study investigates the effects of stand attributes and skid trail area on ground flora diversity at the stand scale. The classification of the ground flora into ecological groups is a basic, yet important, step to better document biodiversity responses that may in turn help us to understand the mechanisms behind those effects (e.g. Gosselin 2012). Indeed, species with similar environmental affinities or which grow in similar conditions are likely to have consistent responses to similar disturbances (Pregitzer et al. 2001; but see for example Godefroid et al. 2005 for contrary results). Previous studies found more shade-intolerant, non-forest species or tree seedlings along skid trails (Buckley et al. 2003; Godefroid and Koedam 2004; Swaine and Agyeman 2008; Zenner and Berger 2008). We therefore retained light demand, successional status and life form as three important plant species traits which may be involved in vegetation response to skid trails. Three questions were asked: (1) What are the respective single and combined effects of stand attributes and skid trail area on understory diversity? (2) Do life form, light preference and successional status determine the direction and magnitude of the ground flora response? (3) Do stand attributes and skid trails have strong effects on the abundance of individual species?

Materials and methods

Study area

The Montargis forest (48°01' N, 2°48' E, Loiret, France) is an ancient state forest (dating back to the 9th century at least), managed by the French National Forestry Office (ONF), which covers 4090 ha and is located in the northern half of France. The elevation ranges from 95 to 132 m a.s.l. The climate is oceanic with a mean annual rainfall and temperature of about 647 mm and 10.9 °C, respectively (Chevalier 2003). The parent rock is Senonian chalk (late Cretaceous), covered with postglacial (Holocene) deposits of diverse textural properties, sand being dominant in the western part and silt in the eastern part. The dominant tree species are sessile oak [*Quercus petraea* (Mattus.) Liebl.], hornbeam (*Carpinus betulus* L.) and beech

(*Fagus sylvatica* L.).

Historically, forest management applied the coppice-with-standards (CWS) system with sessile oak as standards and hornbeam as coppice (Jarret 2004). In this silvicultural system, oaks are allowed to grow to their full height for use as structural timber, while hornbeam is cut at 10-15 year intervals to provide fuel wood or fencing, etc. Currently, the majority of coppice-with-standards stands have not been managed as CWS for decades and are gradually being converted to – mostly even-aged – high forest systems. Generally, the CWS undergo two stages to become a mature even-aged high forest: 1) every ten years, low intensity improvement cuts are carried out to maintain 50 mature oaks per hectare with a DBH between 60 and 80 cm; 2) during a final 10-year period, three to four regeneration fellings remove the shelter of mature trees to trigger natural oak regeneration (Jarret, 2004). Subsequently, the oak saplings gradually develop into mature high forest with a relatively closed canopy. In the region, an oak high-forest rotation is typically 180 to 200 years (Jarret 2004), and regular thinnings are conducted during this cycle to control tree species, tree spacing and tree shape. Regular thinning begins at a stand age of around 40 years old, and the time interval for regular thinning is about every 8-12 years.

Data collection

Data collection was conducted in 1999 by one of the authors (R. Chevalier). Sampling plots (n=96) were selected for the primary purpose of covering four main forest types in the research area corresponding to the different stages of the management cycle (three different even-aged high forest types and one CWS forest type). The three forest types in the first half of the high forest cycle were distributed around the first (SH), third (PH) and sixth thinning (MF). Regarding CWS plots, they were partly selected to represent different forest types based on diameter distributions (with irregular stand structure, medium-diameter regular stand structure and large-diameter regular stand structure respectively). Within each stand type, plot locations were unrelated to skid trail locations. Incidentally, skid trail area varied among plots from relatively low to high (e.g. varied from 0 to 47 %, Table 1). Since plot selection was done independently of skid trailarea, we assume that our plots are representative of the level of skid trailarea for the different forest types studied (cf. Table 1). Time since the last machine entry for thinning was 1 year in sapling high forests (SH) and 2-8 years, 3-7 years and 2-13 years for the other three stand types (PH, MF and CWS) respectively (French National Forestry Service ONF data).

In our study, plot size was 400 m^2 for vegetation sampling and up to 1300 m^2 for large tree sampling. Site type was controlled to avoid site bias among forest types: variations among the variables related to site type were not significantly strong except for sand content which was higher in mature high stands (64 %) than in the other stand types (46 to 55 %). Soil sand content was higher in older high-forest stands. The range of sand content was larger for CWS stands than for the other three high forest stands (Fig. SM 1). To inventory trees, we set up a 22-m-radius circular plot with a 20 m × 20 m square plot nested within it in each stand (Chevalier, 2003). Then we divided the 20 m × 20 m plots into four smaller 10 m × 10 m quadrats and at the centre of each quadrat, set up three circular plots with radii of 1, 2 and 4 m (Fig. 1). Trees were sampled in the following configurations: (1) four 1-m-radius circles for trees with 0.5 cm ≤ height < 1.3 m; (2) four 2-m-radius circles for trees with height ≥ 1.3 m and diameter at breast height (DBH) < 2.5 cm; (3) four 4-m-radius circles for trees with 2.5 - 7.5 cm DBH; (4) four 10 m × 10 m quadrats for trees with 7.5 - 17.5 cm DBH; (5) the 22-m radius circle for trees with DBH > 17.5 cm.

Vegetation was sampled once between the end of April and the end of July, 2000. We did not sample vegetation in early spring for vernal species since only two vernal species (*Anemone nemorosa* and *Hyacinthoides non-scripta*) are present on the mildly acidic soils in the Montargis forest. Moreover, we were still able to detect these two species during our sampling season, although probably in reduced abundance. In each 20 m × 20 m square plot, all vascular plants below 2 m in height (including tree seedlings and saplings) were identified and recorded (Kerguélen, 1999), following the Braun-Blanquet cover/abundance scale classification where **i** is one unique individual and cover < 5%; **+** is very few individuals and total cover < 5%; **1** is few to many individuals, total cover < 5%; **2** is total cover 5% - 25%; **3** is total cover 25% - 50%; **4** is total cover 50% - 75%; and **5** is total cover ≥ 75%.To estimate the area of skid trails in each plot, we measured the length and width of each skid trail within the 20 m × 20 m plot (see Fig. 2), and calculated the total area covered by skid trails by multiplying the length of the skid trails by their width. The total area per plot was finally transformed into relative area in percentage. The range of skid trail area among plots was low (about 10 % SD, Table 1). Skid trail area was the lowest in CWS among the four stand types ($P < 0.001$), and decreased with increasing age in high forest stands (Fig. 3).

Data analysis

We modelled the responses of the richness and the abundance of ecological groups, and the abundance of individual common species (defined as those with an occurrence of > 25% across all stands) to variables related to stand attributes (age, stand type, basal area), skid trail area, sand content and sampling date (Table 1) at the 400-m^2 scale. Sand content was the only soil type variable selected since it was the only one to strongly vary among stand types (Chevalier, 2003) (non-selected variables were soil silt, clay and gravel contents). Sampling date was also used as a covariable in all the models since the cover percentage of certain plant species probably changed during the three-month vegetation sampling period.

Only three (tree) species in the data set (*Picea abies*, *Pinus sylvestris Robinia pseudoacacia*) were introduced species (Muller 2004; Vahrameev and Nobilliaux 2013), and they were infrequent (occurring in 1 to 3 plots at most) and sparse (cover < 1 %). All the other plant species in our research area were native species. Ground flora richness and abundance were calculated by considering groups of species classified according to successional status (SUCC) and light preference (LIGHT), each crossed with life form. We separated woody species from herbaceous species because previous studies had evidenced different response to environmental gradients between these two categories (Barbier et al. 2009, Zilliow & Gosselin 2014). For successional status, we classified the species into three groups following Julve (2002) as in Barbier et al. (2009): (i) mature forest species whose preferred habitat is mature forests, (ii) peri-forest species whose habitats are found close to mature forests either successionally and temporally (shrubs, heathlands, early stages of forest succession) or spatially (along edges, clearings and forest gaps), and (iii) non-forest species whose preferred habitats are not linked to forests. We also distinguished three groups for vascular plants according to light preference (Ellenberg indicator value L, Ellenberg et al. 1992): shade-tolerant ($L < 5$); intermediate light ($5 \leq L < 7$), and heliophilous ($L \geq 7$). These two classifications – successional status and light preference – were distinguished in each of the following life form groups: woody species and herbaceous (i.e. non-woody vascular) plants. The cover/abundance scale coefficients (i, +, 1, 2, 3, 4 and 5) were transformed into percentage cover classes as follows: i to 0.1 %; + to 0.5 %; 1 to 5 %; 2 to 17.5 %; 3 to 37.5 %; 4 to 62.5 %; 5 to 87.5 %.

We applied a total of seven explanatory models to both the richness and abundance of each ecological group (10 groups), and to the abundance of each individual species (13 species, with an occurrence > 25%). The models considered either (a) no effect (null model), four stand attributes (age, stand type, basal area or sand content) and skid trail area, or (b) a combination of effects, including those in the best models from (a) and the effect of skid trail area. If the dominant factor was already skid trail area, we chose the second best explanatory variable among the stand attributes (Age, STP and Gcompo) and then incorporated skid trail area into the model as an additional covariate. Sampling date as a covariate was incorporated in both models (a) and (b) (see Table 1 for more information on these variables). Comparing models (a) helped us distinguish the dominant factor for ground flora diversity, while models (b) were used to further detect the combined effects of stand attributes and skid trail area. The statistical models were quasi-Poisson generalized linear models (glm) for coefficient estimation (McCullagh 1983) and Poisson glm for the model comparison with QAICc (Quasi Akaike Information Criterion corrected for small sample size, Lee and Tsai 1998) with a common dispersion parameter for all the models being compared. We used two different (although related) distributions because species counts could not be strictly assumed to follow a Poisson distribution and QAICc cannot be calculated for quasi-Poisson models. The link function was the default (log) for these models. The common dispersion parameter was taken to be that of the quasi-Poisson basal area by tree species Gcompo model (see Table 1 for a definition of this model).

Analyses based only on statistical significance (*P*-values) are unable to distinguish some practically important trends. This is because, in the usual statistical tests for trends, the failure to reject the null hypothesis of no trend does not prove that the null hypothesis is true, nor does the rejection of the null hypothesis indicate whether or not the trend is ecologically important or non-negligible. The important question is actually whether the true trend is ecologically negligible or not (Dixon and Pechmann 2005). As did Barbier et al. (2009), we distinguished, for both richness and abundance data, two levels of ecological negligibility in the multiplier of the mean of species richness and abundance – here denoted by β – to a given increase in an ecological variable (see below): a more stringent one (b1), corresponding to a strict ecological negligibility and a less stringent one (b2, with $0 < b1 < b2$). Four different cases occur when describing negligibility effects: (1) negligible weak effects denoted by “0” when the value of the multiplier (β) follows $P(-b2 < \log(\beta) < b2) \geq 0.975$, and negligible very weak effects denoted by "00" for the more stringent $P(-b1 < \log(\beta) < b1) \geq 0.975$; (2) non-negligible negative and very negative effects: "-" for $P(\log(\beta) < -b1) \geq 0.975$ and "--" for the stronger $P(\log(\beta) < -b2) \geq 0.975$; (3) non-negligible positive and very positive effects: "+" for $P(\log(\beta) > b1) \geq 0.975$ and "++" for the stronger $P(\log(\beta) > b2) \geq 0.975$; and (4) inconclusive cases where the estimator cannot be classified in any of the above categories (no symbol). In our study, negligible weak (or very weak) effects will be called weak (or very weak) effects; non-negligible negative (or very negative) effects will be called negative (or strongly negative) effects; and non-negligible positive (or very positive) effects will be called positive (or strongly positive) effects (see Table SM 1. in Supplementary Material). In our analysis, we chose b1 = 0.1, b2 = 0.2 for species richness, and b1 = 0.25, b2 = 0.5 for abundance, as in Barbier et al. (2009). In other words, we considered that a change of 10 % in species richness or 25 % in abundance was an ecologically-important change, while a change of 20 % or 50 % respectively was a strongly important change. To gauge the negligibility of the effects, we considered the equivalent of about one standard deviation for the increase in the continuous ecological variables: 20 years increment for age, 5 $m^2 ha^{-1}$ for basal area, 10 % for skid trail area, 11 % for sand content and 30 d for sampling date. For stand type (STP), we calculated the associated multiplicative coefficient by supposing the stand changed from one type to the next type during forest succession: coppice-with-standards stands to sapling high forest (STP_{CWS-SH}), sapling to pole stage in even-aged stands (STP_{SH-PH}), pole to mature stage in even-aged stands (STP_{PH-MH}), and mature even-aged forest to coppice-with-standards stands (STP_{MH-CWS}). For each variable, we reported the mean value of the multiplier, its 97.5 % confidence interval, and the probability of the significance test that the parameter was null. Levels of statistical significance for parameters were symbolized as follows: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$.

To determine whether there were any effects of skid trails on species composition other than species richness, we performed a partial Mantel test of the correlation between the Jaccard dissimilarity matrix and the difference between plots in the presence of skid trails (Mantel 1967; Legendre and Legendre 1998). To perform the partial Mantel test, we used a modified function of the R Vegan package. We removed the effects of stand type to detect whether there was a significant difference in species composition between plots with skid trails and plots without skid trails inside each stand type. The significance of the calculated correlations was determined through re-sampling techniques by running 1000 random plot permutations inside each stand type in one of the distance matrices (the Jaccard dissimilarity matrix or the matrix of the difference between plots in the presence of skid trails) and by generating a null distribution of correlation values from these permutations.

We used generalized linear models (GLMs) with the Gaussian “family” to assess the association between skid trail area and stand type.

Results

When we compared the total richness/total abundance between plots with and without skid trails, plots with skid trails were found to have either higher total abundance or mean richness/total abundance than plots without skid trails (Fig. SM 2 and Table SM 2). Total (or mean) richness and abundance decreased with increasing age of high-forest stands (Table SM 2 and Fig. SM 3). In CWS plots, the total (or mean) richness and abundance was higher than in mature high stands (MH) but lower than in sapling (SH) and pole-stage high stands (PH) (Table SM 2. and Fig. SM 3). There was no significant relationship between total richness (or total abundance) and sand content (Fig. SM 3).

Results at the ecological group level

Models related to stand type were the best models for richness for all ecological groups (Table 2). For abundance data, the best models for woody plants were related to either stand type or skid trail area (Table SM 3). For example, stand type was the best model for peri-forest (PF) and intermediate-light (INT) woody species, and skid trail area was the best model for mature forest (MF) and heliophilous (HEL) woody species. For all the herbaceous groups, on the other hand, the best model was basal area by tree species (Gcompo).

We have summarized the effects of the variables on the richness and abundance of herbaceous plants according to magnitude analyses (Table 3 and Table SM 4). Negative (or strongly negative) effects include: 1) stand age (Age) (except for peri-forest species abundance), 2) pole stage high forest compared to sapling high forest ($STP_{SH\text{-}PH}$) (except for non-forest species abundance and heliophilous species richness and abundance), 3) mature stage high forest compared to pole stage high forest ($STP_{PH\text{-}MH}$) (except for peri-forest species abundance and intermediate-light species richness and abundance), and 4) basal area of beech (G_B) and hornbeam (G_H) (except for non-forest and heliophilous species abundance). Positive (or strongly positive) effects include: 1) sapling high stands compared to coppice-with-standards stands ($STP_{CWS\text{-}SH}$) (all herbaceous groups), 2) coppice-with-standards stands compared to mature high stands ($STP_{MH\text{-}CWS}$) (only for HEL species abundance) and skid trail area. Weak or inconclusive effects were found for basal area of sessile oak (G_O) and sand content. Sampling date as a covariable had a positive effect on MF and shady (SHA) herb richness in the model combining Gcompo and sampling data; sampling date also had a negative effect on HEL abundance in the model combining stand type and sampling date.

Compared to herbaceous plants, however, woody plants showed very weak responses to stand age (Table 3 and Table SM. 5 in Supplementary Material). Indeed, not all the woody SUCC and LIGHT ecological groups were negatively affected by $STP_{SH\text{-}PH}$, $STP_{PH\text{-}MH}$ G_B and G_H. For example, $STP_{SH\text{-}PH}$ had a negative effect on HEL abundance, $STP_{PH\text{-}MH}$ had negative effects on PF and INT species richness and abundance (Table 3 and Table SM. 5 in Supplementary Material).$STP_{MH\text{-}CWS}$ showed positive effects on the richness and abundance of PF and INT woody species. The effect of skid trail area was weak for all the woody groups, and sand content had a negative effect on PF richness. The effect of sampling date on woody plants was weak.

For both woody and herbaceous plants, adding skid trail area as an additional effect to the best tree-stand indicators (Table 4 and Table SM 5) only slightly affected the estimated effects of tree stand variables; furthermore, even on herbaceous species, the positive effect of skid trail area turned out to be weak. The effects of sampling date in the additive models were weak for both woody and herb species.

Species level results

For the thirteen species whose occurrence was more than 25 % (Table 5 in Supplementary Material), seven species (*Carpinus betulus, Fagus sylvatica, Carex pilulifera, Deschampsia flexuosa, Festuca heterophylla, Holcus mollis* and *Teucrium scorodonia*) had best models related to basal area by tree species (Gcompo); five species (*Quercus petraea, Hedera helix, Ilex aquifolium, Lonicera periclymenum* and *Rubus fruticosus*) had best models related to stand type; one species (*Sorbus torminalis*) had no best model related to the variables in our study.

We analysed the magnitude and negligibility of the effects of stand attributes and skid trail area on the abundance of individual species (excluding *Sorbus torminalis* because it had no best model related to the variables in our study; Table 6. A and 6.B). Contrary to the results at the ecological group level where age effects were frequently negative, age had weak effects at the species level (except for *Teucrium scorodonia*). Furthermore, $STP_{SH\text{-}PH,}$ $STP_{PH\text{-}MH,}$ and G_B did not always show negative effects as they did at the ecological group level: for some species, their effects were even positive. For example, $STP_{SH\text{-}PH}$ had positive effects on *Hedera helix, Lonicera periclymenum* and *Rubus fruticosus, and* $STP_{PH\text{-}MH}$ had positive effects on *Fagus sylvatica* and *Quercus petraea.* In addition, negative responses to $STP_{CWS\text{-}SH}$ were found at the species level (*Fagus sylvatica* and *Hedera helix*). At the species level, the effects of G_H were weak except for *Deschampsia flexuosa* and *Teucrium scorodonia*. Although skid trail area had positive effects on *Quercus petraea*, *Deschampsia flexuosa* and *Teucrium scorodonia* and a negative effect on *Fagus sylvatica*, in the models combining the best tree variable with skid trails, the effects of skid trail area became inconclusive (Table SM. 6.A and 6.B). Soil sand content and sampling date effects were weak for all the species investigated.

Mantel test

Finally, the partial Mantel test removing the effects of stand type revealed a significant difference in species composition between plots with skid trails and those without skid trails ($r = 0.1788$, $p < 2.22e\text{-}16$).

Discussion

Ground flora diversity is mainly driven by stand attributes

Though the effects of stand attributes and skid trails have been studied, no previous study has ever combined the two factors to detect their effect at the stand scale. In our study, stand type was the best indicator of ground flora richness. For abundance, stand type, basal area of tree species or skid trail area was best, depending on the ecological traits of the ground flora. In previous studies, age, stand type and basal area or other tree stand variables have been directly or indirectly found to be important factors impacting understory diversity (Nagaike et al. 2005; Baeten et al. 2009; Duguid and Ashton 2013) in managed forest, but few (Barbier, et al. 2009; Zilliox and Gosselin 2014) compared those important variables to detect which one might be the best indicator under the multiple hypotheses framework (Chamberlin 1965).

Typical CWS forests can provide a wide variety of environmental conditions (e.g. light, temperature, soil acidity) due to regular harvesting among stands. The conversion of traditional CWS forests to high forest could cause significant changes in forest plant diversity in Europe (Van Calster et al. 2007; Baeten et al. 2009). Yet changes in diversity also depend on the attributes (e.g. un-even or even-aged) of the high forest that results from the conversion. For example, Baeten et al. (2009) found that the abandonment and conversion of CWS forest to un-even aged high forest increased total plant diversity, while Van Calster et al. (2007) showed that ground flora diversity decreased shortly after conversion from CWS to even-aged high forest at an early succession stage (28 years old). However, when focusing on forest management conversion to even-aged high forest, few studies compared both early and late succession forest with CWS forest to better understand diversity changes during the transition. Like the work done by Duguid and Ashton (2013), our study included both short- and long- term diversity response to the conversion from CWS to even-aged high forest. Duguid and Ashton (2013) and our study found no decrease in ground flora diversity in the early stage of succession: herbaceous species diversity increased considerably in our study, whereas it did not change significantly in Duguid and Ashton (2013). The CWS forest in our study – unlike a typical CWS forest in Van Calster et al. (2007) – is no longer being regularly cut and may therefore be more similar to the forests described by Duguid and Ashton (2013) prior to major harvesting disturbance. This may explain the difference in our results with those of Van Calster et al. (2007). However, both our study and Duguid and Ashton's (2013) did show a decrease in plant diversity long after (i.e. more than 50 years) conversion to even-aged high forest. In our study, the richness of peri-forest and intermediate-light woody species, and the abundance of heliophilous herbaceous species, remained higher in CWS compared to mature even-aged high forest. Concerning the species groups that favoured CWS forest, previous studies comparing the diversity in typical CWS forests (with regular cutting) and in high forests also found more heliophilous species in CWS stands (Van Calster et al. 2007). Other ecological groups which were not included in our research such as vernal species and seed banking species have also been found to benefit from the CWS disturbance regime (Peterken 1981). Finally, the species richness of nearly all the herbaceous species groups in our study increased dramatically during the early stage of the conversion from CWS to a regular high-forest system.

In our study, the aging process from young to mature even-aged high forest stands is accompanied by a decrease in ground flora diversity, and this decrease tends to be sharper from pole to mature stage than from sapling to pole stage. Decreases in species richness in mature stands compared to young stands were also found in the studies by Small and McCarthy (2005). Duguid and Ashton (2013) concluded that the decrease was mainly due to the fact that old stands become more homogeneous in structure, resulting in more uniform microhabitats, as they mature from even-aged young stands. Some other studies, though not based on the same traits, classified ground flora into ecological groups and detected variations among groups in their response to forest age. For example, Massant et al. (2009) found higher proportions of stress-tolerant species in pure 100-to-150-year-old beech stands than in younger and older stands (5 age classes, intervals of 50 years). The study by Brockerhoff et al. (2003) distinguished adventive (25.7 %) and indigenous species and found that the richness and cover of indigenous species were the highest in the oldest stands. Furthermore, the abundance measured in these studies was relative abundance whereas we measured absolute abundance. In our study, the decrease in understory diversity in older forests was parallel to a decrease in all herbaceous groups and peri-forest and intermediate-light of woody species.

However, changes in ground flora diversity during the stand maturing process might be clearer at the species level than at the ecological group level. This was what Godefroid et al. (2005) found: species from the same humus type did not show the same response to stand aging. In our study, we did not detect such a discrepancy for the effect of age – all the investigated species showed a weak response to age (except for *Teucrium scorodonia*). However, we did observe a difference in stage effect at species and ecological group levels for woody species. Indeed, at the ecological group level, the abundance of intermediate-light woody species significantly decreased from sapling to pole stage. Yet the response to stand stage from sapling to pole stages varied among woody species that belonged to the same intermediate-light species group: the abundance of *Rubus fruticosus* increased, while that of *Ilex aquifolium* decreased; and one species showed an inconclusive response (*Lonicera periclymenum*). However, the herbaceous species response to stand transition from sapling to pole stage was consistent at both ecological and species level. For example, *Carex pilulifera* , *Deschampsia flexuosa* , *Holcus mollis* and *Teucrium scorodonia* all belong to the intermediate-light herbaceous group and all had negative responses to stand transition from sapling to pole stage; the negative response was also found at the ecological group level.

It is generally considered that hardwood forests host a higher diversity of vascular plants than do coniferous forests (Augusto et al. 2003; Barbier et al. 2008). However, the review by Barbier et al. (2008) showed that few studies had actually compared vascular plant diversity among different hardwood (or coniferous) forest types (Nagaike et al. 2005; Barbier et al. 2009; Massant et al., 2009). Our study compared the relative effect of the basal area of oak, beech and hornbeam in an oak-dominant forest. The richness and abundance of all the herbaceous ecological groups were negatively influenced by the basal area of beech and hornbeam but did not respond to that of oak. The negative effect of beech on understory diversity has been found in studies that compared oak to beech stands (e.g. Nagaike et al. 2005), and a similar negative effect for hornbeam can also be found in Kwiatkowska et al. (1997), and to some extent in Barbier et al. (2009).

Limited additional effect of skid trails on ground flora diversity

Skid trails have been found to impact soil and vegetation at the small scale (e.g. on the skid trail, Buckley et al. 2003; Demir et al., 2007; Lotfalian and Bahmani 2011; Wei et al. 2015). We found two studies on the effects of skid trail area at the stand scale. In the study by Berger et al. (2004), species richness was found to be greater on plots (60 m^2) with skid trails than plots off skid trails. Zenner and Berger (2008) found that when 60 m^2 plots were exposed to increasing motor vehicle traffic (i.e., forest floor disturbance) and canopy removal intensity, the ground flora shifted from interior forest species to more ruderal, invasive/noxious, disturbed-forest species. In our study, when focusing only on the single-variable effect of skid trail area, the results were consistent with the above studies that skid trail area promoted the total ground flora diversity at stand scale: more precisely, the richness and abundance of all herbaceous groups (except for heliophilous species abundance) strongly increased with increasing skid trail area.

Yet, the incorporation of skid trail area as an additional effect into our best tree-stand models did not lead to a significant improvement in the models' ability to explain variations in ground flora diversity. This discrepancy between single variable and multi-variable results can be explained by differences in skid trail area among stand types (Fig. 3). The single effects detected were in fact mainly due to differences in skid trail area among stand types and were better accounted for by stand type effects. This might be due to our sampling scheme since our sample plots were selected to cover different stand types but not the largest possible gradient of skid trail area among plots (about 10 % SD, Table 1). Indeed, even if the effect of skid trail area is consistent and strong across stand types, it may be ill estimated due to too small a gradient of skid trail area. This would engender too much noise for the estimators to be conclusive; and that is indeed what we mostly observed (cf. Table 4). This does not mean that the estimators indicate a weak effect. It is therefore possible that larger variations in skid trail area in each stand type would have given clearer results, indicating either strong or weak effects of skid trail area on floristic biodiversity, even after taking into account stand type.

Nevertheless, the results of the partial Mantel test indicated a significant difference in species composition between plots with skid trails and plots without skid trails, after the effect of stand type was removed. In other words, some species were sensitive to skid trails at the stand scale, but we had difficulties interpreting which species were involved. Indeed, as we did not observe any response to skid trail area in the additive models at the ecological group level based on light requirements and successional status, we could not simply predict the response of species to skid trail area from these two traits. Godefroid and Koedam (2004) showed that the abundance of 61 % of the species studied was significantly related to soil compaction (10 m^2 plots). We therefore assumed that individual species would show a significant response to the effects of skid trail area at the stand scale. However, the best models at the species level (for species with at least 25% occurrences) were related to tree stand properties (stand type, total basal area of oak, beech and hornbeam or sand content), with results similar to those at the ecological group level. For the effects of skid trail area in the model combining stand attributes and skid trail area, the abundance of eight out of twelve species were not affected by skid trail area, while the remaining four species showed inconclusive results.

Management implications and suggestions to further investigation

Our study compared the respective and combined effects of models related to stand attributes and skid trail area on biodiversity at both the ecological group level and the individual species level at the stand scale. We concluded that ground flora was mostly affected by stand type or basal area, while skid trail area showed weak effects on ground flora diversity. Ground flora species, especially herbaceous species, were progressively lost with the development of high forest rotation (≤ 104 yr). Two management implications stem from our findings. First, the development of mechanized harvesting may not strongly destabilize plant communities in the short term at the stand scale, at least at the level of intensity currently observed in the Montargis forest. Networks comprised of road and skid (or tractor) trails are requisite features in forests managed for timber harvesting (Buckley et al. 2003; Avon et al. 2013). In previous studies, sampling has often focused on skid trails that have been subjected to rather high levels of disturbance. Conclusions about skid trail effects studied in such areas may have overemphasized the severity of impact of skidding traffic at the stand or landscape scale (Zenner et al. 2007). In our research area, mean skid trail area/density was observed to be low compared to other research areas. Moreover, the extremes associated with highly disturbed stands are not found in this forest, though local compaction levels in our study area were (slightly) above the threshold value at which root growth is restricted (Wei et al., 2015) (between 2500 and 3000 kPa, depending on species, soil type, and penetrometer characteristics; the value of 3000 kPa is often found to be the threshold of restricting root penetration into sandy soil) (Taylor et al., 1966; Sands et al. 1979).

Second, our results indicate that long forest rotations and stands with high basal area for hornbeam or beech may negatively affect herbaceous diversity at the ecological group level. However, there were some limitations in our study – the main one being that sampling was done only the first half of the rotation. The phenomenon of species loss may continue at a lower rate, may stabilise or may even reverse during the second half of the cycle.

Furthermore, in the near future, the management plan is likely to call for thinning to reduce oak competition for water in summer, and this may favour heliophilous species, peri-forest or non-forest species later on in the cycle. On the other hand, transforming CWS to an even-aged high-forest regime in the Montargis forest is causing a long-term decrease in peri-forest and intermediate-light woody species, and in heliophilous herbaceous species. These species might not find the same favourable conditions in the new regular high stands, except perhaps at the very beginning of the high forest cycle for heliophilous species. Therefore, further studies during the second half of the forest cycle are needed, as is assessing the impact of limiting oak stem density on ground flora diversity. Long-term or spatial studies are also needed, to better understand whether a short-term increase in floristic biodiversity, at the very beginning of the even-aged high forest cycle, could maintain the diversity of these species at the landscape scale or in successive even-aged cycles.

Furthermore, the results showed that sampling date is a significant predictor variable for the richness of mature-forest and shade-tolerant and the abundance of heliophilous species, suggesting that plant phenology and sampling date should be taken into account when analysing plant data taken early and late during the sampling season. Finally, our study was in agreement with Barbier et al. (2009) and Zilliox and Gosselin (2014) who found that the responses of woody and herbaceous ecological groups to the different variables diverged. We therefore suggest separating woody and herbaceous species before classifying the ground flora into different ecological groups in future studies on the effects of forest management on floristic biodiversity.In the coming years, French silviculture is likely to substantially change due to global warming and biomass fuel needs: shorter rotations, increased timber harvesting and more frequent penetration of logging vehicles can be expected (Avon et al. 2013). We recommend further investigations in contexts: 1) in the second half of the forest rotation (>104 yr), and cover a wider range of skid trail area; 2) where invasive and/or undesirable (highly competitive) plants are present, 3) where soils are more prone to compaction, and 4) with other spatial scales and over a longer time period.

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Table 1

Description and statistical summary of the ecological variables used in the models

Variable	Description	Mean	SD	Range
Age	High-forest stand age (year or class)	71.83	33.77	13-126
STP	Stand type (4 types): 3 even-aged high forest (HF) types: SH: 34 years old (12 plots), PH: 55 years old (24 plots), MH: 104 years old (12 plots); and 1 coppice-with-standards (CWS) type (48 plots)	---	---	---
G	Total stand basal area at breast height of total tree stands (m^2/ha)	24.24	7.31	0.07-35.70
Gcompo	G_O+G_B+G_H (G_O: G of oak; G_B: G of beech; G_H: G of hornbeam (m^2/ha)	G_O:18.02 G_B:1.91 G_H:4.31	7.29 2.21 4.51	0.07-32.03 0.024-8.69 0.098-19.51
AST	Relative area of skid trails within plot (%) (Fig.2)	SH: 27.19 PH: 5.57 MH: 3.37 CWS: 0.50	11.00 5.05 5.29 1.84	15.00-47.48 0.00-20.71 0.00-15.00 0.00-9.19
Sand	Soil sand content (%)	50.37	11.39	26.00-73.60
Date	Vegetation sampling date (d)	48	28	26 Apr-27 Jul

Table 2
Differences in QAICc values between the different ecological models and the null model (with sampling date as covariables in all models) for ecological group richness (see also Table 1)

	Woody species				Herbaceous species					
	SUCC		LIGHT		SUCC			LIGHT		
	MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age	1.82	0.06	2.12	-6.02	-111.02	-57.15	-100.39	-72.43	-58.67	-65.67
Standtype	**-13.96**	**-19.97**	**-22.27**	**-18.15**	**-133.50**	**-69.73**	**-116.22**	**-89.83**	**-82.55**	**-81.22**
Gcompo	-0.01	-0.19	4.28	-9.66	-132.51	-60.30	-98.83	-96.02	-66.92	-58.24
AST	1.53	-2.18	2.04	-4.36	-84.67	-50.58	-71.92	-65.46	-65.77	-35.50
Sand	-4.19	-18.62	-18.80	-4.53	0.68	1.85	-3.59	1.38	0.41	-1.86

SUCC: succession status, LIGHT: light preference. MF: mature forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. The smaller the QAICc, the better the model with respect to the others. Within each ecological group, the model with the smallest QAICc is in bold.

Table 3

Multiplicative effect of a substantial variation in ecological variables on the richness of the ecological groups

Models	Variables	Woody species				Herbaceous species					
		SUCC		LIGHT		SUCC			LIGHT		
		MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age+Date	Age(+20yr)	0.99^{00} [0.97;1.02]	0.95^{0} [0.88;1.02]	1.00^{00} [0.96;1.04]	$0.96^{**,00}$ [0.92;0.99]	$0.73^{***,--}$ [0.68;0.78]	$0.81^{***,-}$ [0.77;0.86]	$0.72^{***,--}$ [0.67;0.77]	$0.70^{***,--}$ [0.63;0.77]	$0.81^{***,-}$ [0.76;0.85]	$0.71^{***,--}$ [0.66;0.77]
	Date(+30d)	$1.07^{**,0}$ [1.02;1.12]	1.02^{0} [0.89;1.16]	1.05^{0} [0.98;1.13]	1.04^{0} [0.98;1.11]	1.24^{**} [1.09;1.41]	1.04^{0} [0.94;1.16]	1.05^{0} [0.92;1.2]	$1.41^{**,+}$ [1.15;1.72]	1.02^{0} [0.91;1.13]	1.11 [0.95;1.3]
STP+Date	STP_{CWS-SH}	0.94^{0} [0.83;1.08]	1.33 [0.98;1.81]	1.00 [0.83;1.19]	1.24^{**} [1.06;1.44]	$4.1^{***,++}$ [3.2;5.24]	$2.64^{***,++}$ [2.11;3.29]	$4.20^{***,++}$ [3.24;5.43]	$5.03^{***,++}$ [3.48;7.25]	$2.87^{***,++}$ [2.35;3.5]	$4.15^{***,++}$ [2.99;5.77]
	STP_{SH-PH}	1.13 [0.98;1.3]	0.79 [0.57;1.11]	0.94 [0.77;1.15]	0.92 [0.78;1.08]	$0.57^{***,--}$ [0.45;0.72]	$0.6^{***,--}$ [0.47;0.75]	$0.59^{***,--}$ [0.46;0.76]	$0.46^{***,--}$ [0.32;0.65]	$0.47^{***,--}$ [0.38;0.58]	0.77 [0.58;1.04]
	STP_{PH-MH}	0.85^{*} [0.72;1]	$0.34^{***,--}$ [0.2;0.6]	$0.64^{***,-}$ [0.5;0.83]	0.78^{*} [0.63;0.95]	$0.43^{***,--}$ [0.28;0.67]	$0.61^{**,-}$ [0.43;0.88]	$0.33^{***,--}$ [0.21;0.53]	$0.38^{*,-}$ [0.18;0.82]	0.71^{*} [0.51;0.99]	$0.21^{***,--}$ [0.11;0.39]
	STP_{MH-CWS}	1.11 [0.96;1.27]	$2.75^{***,++}$ [1.65;4.59]	$1.66^{***,++}$ [1.33;2.08]	1.14 [0.95;1.36]	0.99 [0.65;1.51]	1.03 [0.75;1.42]	1.22 [0.79;1.88]	1.15 [0.54;2.42]	1.06 [0.79;1.42]	1.50 [0.82;2.73]
	Date(+30d)	$1.05^{*,0}$ [1;1.1]	0.96^{0} [0.85;1.1]	1.02^{00} [0.95;1.09]	1.03^{00} [0.97;1.1]	1.22^{**} [1.07;1.41]	1.05^{0} [0.93;1.17]	0.99^{0} [0.86;1.15]	$1.44^{**,+}$ [1.16;1.79]	1.05^{0} [0.95;1.17]	0.98 [0.81;1.17]
GB+Date	GB(+5m^2/ha)	0.94^{0} [0.85;1.03]	0.70^{*} [0.53;0.93]	0.90 [0.78;1.05]	$0.79^{***,-}$ [0.7;0.89]	$0.37^{***,--}$ [0.28;0.48]	$0.51^{***,--}$ [0.41;0.63]	$0.33^{***,--}$ [0.24;0.46]	$0.28^{***,--}$ [0.19;0.42]	$0.54^{***,--}$ [0.43;0.68]	$0.32^{***,--}$ [0.21;0.47]
	GH(+5m^2/ha)	1.03^{00} [0.98;1.08]	0.93 [0.81;1.07]	1.02^{00} [0.94;1.1]	0.96^{0} [0.9;1.02]	$0.62^{***,--}$ [0.54;0.71]	$0.77^{***,-}$ [0.69;0.85]	$0.66^{***,--}$ [0.57;0.76]	$0.64^{***,--}$ [0.54;0.76]	$0.73^{***,-}$ [0.65;0.82]	$0.66^{***,--}$ [0.56;0.79]
	GO(+5m^2/ha)	$1.03^{*,00}$ [1;1.06]	0.99^{00} [0.91;1.07]	1.00^{00} [0.96;1.05]	1.01^{00} [0.97;1.05]	$0.89^{***,0}$ [0.85;0.94]	$0.90^{***,0}$ [0.85;0.94]	$0.93^{*,0}$ [0.87;0.99]	$0.83^{***,0}$ [0.81;1.01]	$0.89^{***,0}$ [0.85;0.94]	0.95^{0} [0.88;1.02]
	Date(+30d)	$1.07^{**,0}$ [1.02;1.11]	1.03^{0} [0.9;1.17]	1.05^{0} [0.98;1.13]	1.05^{0} [0.99;1.11]	$1.39^{***,++}$ [1.23;1.58]	1.14^{*} [1.03;1.26]	1.16^{*} [1.01;1.33]	$1.73^{***,++}$ [1.43;2.09]	1.11 [0.99;1.23]	1.22^{*} [1.03;1.45]
AST+Date	AST (+10%)	0.98^{00} [0.94;1.03]	1.12^{*} [1.01;1.24]	1.01^{00} [0.95;1.08]	$1.07^{*,0}$ [1.01;1.12]	$1.41^{***,++}$ [1.31;1.53]	$1.33^{***,++}$ [1.25;1.42]	$1.40^{***,++}$ [1.29;1.53]	$1.51^{***,++}$ [1.37;1.67]	$1.35^{***,++}$ [1.26;1.44]	$1.38^{***,++}$ [1.25;1.53]
	Date(+30d)	$1.08^{**,0}$ [1.03;1.13]	1.03^{0} [0.91;1.17]	1.05^{0} [0.98;1.12]	$1.06^{*,0}$ [1;1.12]	$1.39^{***,+}$ [1.22;1.6]	1.12^{*} [1.01;1.23]	1.20^{*} [1.04;1.39]	$1.61^{***,++}$ [1.33;1.94]	1.09^{0} [0.98;1.21]	1.28^{**} [1.08;1.52]
Sand+Date	Sand (+11%)	$0.95^{*,00}$ [0.91;0.99]	$0.77^{***,-}$ [0.69;0.85]	0.86^{***} [0.82;0.91]	$0.94^{*,0}$ [0.89;0.99]	0.95 [0.82;1.09]	1.03^{0} [0.92;1.16]	0.88 [0.76;1.03]	0.94 [0.78;1.14]	0.94^{0} [0.84;1.07]	0.88 [0.74;1.04]
	Date(+30d)	$1.08^{***,0}$ [1.03;1.13]	1.09 [0.97;1.23]	$1.07^{*,0}$ [1.01;1.14]	$1.08^{**,0}$ [1.02;1.14]	$1.44^{***,++}$ [1.23;1.7]	1.17^{*} [1.03;1.34]	1.29^{**} [1.08;1.53]	$1.62^{***,++}$ [1.3;2.01]	1.17^{*} [1.02;1.33]	$1.36^{**,+}$ [1.13;1.64]

Variations were: an addition of 20 years for even-aged high forest age, 5 $m^2\ ha^{-1}$ for basal area data (G_B, G_H, G_O), 10% for skid trail area (AST), 11% for sand content (Sand), 30d for sampling date (Date) and a transition from sapling to pole stage in even-aged forests ($STP_{SH\text{-}PH}$), pole to mature stage in even-aged forests ($STP_{PH\text{-}MH}$) and mature even-aged forest to coppice-with-standards stands ($STP_{MH\text{-}CWS}$). Levels of statistical significance of parameters are symbolized as follows: ***$p<0.001$, **$p<0.01$, *$p<0.05$. ‘‘0’’ and ‘‘00’’ indicate that the effect has a *p*-value of at least 0.975 of being negligible at two different levels. ‘‘$^{-}$’’ and ‘‘–’’ indicate that the effect has a *p*-value of at least 0.975 of being negative and non-negligible at two different levels. ‘‘$^{+}$’’ and ‘‘$^{++}$’’ indicate that the effect has a *p*-value of at least 0.975 of being positive and non-negligible at two different levels (further details are given in the Data analysis section). Values in brackets are 97.5% confidence intervals of the coefficients.

Table 4

Multiplicative effect of the variables of the best model with skid trails on the richness of the ecological groups

Variables	Woody species				Herbaceous species					
	SUCC		LIGHT		SUCC			LIGHT		
	MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age(+20 yr)										
$STP_{CWS\text{-}SH}$	0.94 [0.73;1.21]	1.01 [0.54;1.90]	0.95 [0.66;1.35]	1.15 [0.85;1.56]	$3.39^{***,++}$ [2.18;5.29]	1.62^{*} [1.07;2.47]	$3.84^{***,++}$ [2.42;6.09]	$3.58^{***,++}$ [1.87;6.85]	$2.41^{***,++}$ [1.65;3.53]	$3.31^{***,++}$ [1.84;5.96]
$STP_{SH\text{-}PH}$	1.14 [0.9;1.43]	1.00 [0.57;1.76]	0.98 [0.71;1.36]	0.97 [0.74;1.28]	0.66^{*} [0.45;0.97]	0.89 [0.61;1.29]	0.64^{*} [0.43;0.95]	0.60 [0.35;1.06]	$0.54^{***,--}$ [0.38;0.76]	0.93 [0.57;1.53]
$STP_{PH\text{-}MH}$	0.85^{*} [0.72;1]	$0.35^{***,--}$ [0.2;0.61]	$0.64^{**,-}$ [0.5;0.83]	0.78^{*} [0.63;0.96]	$0.44^{***,--}$ [0.28;0.68]	$0.63^{**,-}$ [0.45;0.89]	$0.33^{***,--}$ [0.21;0.53]	$0.39^{*,-}$ [0.18;0.83]	0.72 [0.51;1]	$0.21^{***,--}$ [0.11;0.4]
$STP_{MH\text{-}CWS}$	1.11 [0.96;1.28]	$2.84^{***,++}$ [1.69;4.77]	$1.67^{***,++}$ [1.33;2.1]	1.15 [0.95;1.37]	1.01 [0.66;1.55]	1.10 [0.81;1.5]	1.23 [0.79;1.91]	1.20 [0.56;2.53]	1.08 [0.8;1.45]	1.54 [0.84;2.81]
G_B(+5m^2/ha)										
G_H(+5m^2/ha)										
G_O(+5m^2/ha)										
AST (+10%)	1.01 [0.79;1.29]	1.36 [0.75;2.48]	1.06 [0.7 5;1.5]	1.09 [0.81;1.46]	1.24 [0.82;1.86]	1.17 [0.78;1.51]	1.11 [0.72;1.7]	1.46 [0.82;2.6]	1.21 [0.85;1.74]	1.29 [0.76;2.19]
Sand(+11%)										
Date(+30d)	1.02^{00} [1.00;1.03]	0.99^{00} [0.94;1.03]	1.01^{00} [0.98;1.03]	1.01^{00} [0.99;1.03]	$1.07^{**,0}$ [1.02;1.12]	1.01^{00} [0.98;1.05]	1^{00} [0.95;1.05]	$1.13^{**,0}$ [1.05;1.21]	1.02^{00} [0.98;1.05]	0.99^{00} [0.93;1.05]

The legend is the same as for Table 3.

Table 5
Differences in QAICc values between the different ecological models and the null model (with sampling date as covariables in all models) for species abundance

	Carpinus betulus	*Fagus sylvatica*	*Quercus petraea*	*Sorbus torminalis*	*Hedera helix*	*Ilex aquifolium*	*Lonicera periclymenum*	*Rubus fruticosus*	*Carex pilulifera*	*Deschampsia flexuosa*	*Festuca heterophylla*	*Holcus mollis*	*Teucrium scorodonia*
Age	-5.19	-22.07	-11.08	2.59	2.20	4.02	-11.43	-13.4	3.41	-22.3	-25.26	-10.56	-59.87
Standtype	-3.39	-26.68	**-67.96**	5.70	**-19.13**	**-2.77**	**-22.54**	**-31.61**	2.70	-29.11	-21.07	-24.40	-61.23
Gcompo	**-17.69**	**-31.54**	-36.54	2.72	-4.45	6.27	-16.71	-13.87	**-5.91**	**-44.03**	**-26.84**	**-24.61**	**-65.06**
AST	-4.57	-15.65	-58.95	3.44	-2.70	2.59	-6.00	-4.17	1.75	-34.64	-8.26	-17.00	-37.41
Sand	2.50	-8.43	3.03	3.96	-0.55	1.41	-6.13	-10.80	1.35	-0.07	-1.92	-3.88	-9.75

The meanings of the Age, STP, Gcompo and AST are in table 1. The smaller the QAICc, the better the model with respect to the others. The model with the smallest QAICc is in bold for each species.

Table 6.A

Multiplicative effect of a substantial variation in ecological variables on abundance of the first half species

Models	Variables	*Carpinus betulus*	*Fagus sylvatica*	*Quercus petraea*	*Hedera helix*	*Ilex aquifolium*	*Lonicera periclymenum*
Age+Date	Age(+20 yr)	$0.88^{*,00}$ [0.8;0.97]	1.42^{***} [1.21;1.65]	$0.84^{**,0}$ [0.76;0.94]	1.02^{00} [0.91;1.13]	0.94^{0} [0.7;1.25]	$0.91^{*,00}$ [0.83;0.99]
	Date(+30d)	1.03^{00} [0.85;1.23]	1.18^{0} [0.95;1.47]	0.97^{00} [0.8;1.18]	1.15^{0} [0.94;1.4]	0.96 [0.56;1.63]	$1.21^{*,0}$ [1.02;1.43]
STP+Date	$STP_{CWS\text{-}SH}$	1.57 [0.98;2.5]	$0.05^{**,--}$ [0.01;0.44]	$3.20^{***,++}$ [2.46;4.16]	$0.29^{**,-}$ [0.12;0.7]	1.88 [0.75;4.73]	1.23 [0.80;1.90]
	$STP_{SH\text{-}PH}$	1.03 [0.64;1.67]	7.39 [0.81;67.06]	$0.15^{***,--}$ [0.1;0.23]	$5.08^{***,++}$ [2.12;12.17]	$0.14^{*,-}$ [0.03;0.69]	1.65^{*} [1.08;2.54]
	$STP_{PH\text{-}MH}$	0.48^{*} [0.24;0.93]	$3.39^{**,+}$ [1.58;7.29]	$2.79^{***,++}$ [1.7;4.57]	$0.26^{**,--}$ [0.12;0.59]	0.24 [0;18.89]	$0.38^{**,-}$ [0.21;0.67]
	$STP_{MH\text{-}CWS}$	1.30 [0.71;2.38]	0.78 [0.45;1.34]	0.73 [0.5;1.05]	2.56^{*} [1.2;5.47]	16.01 [0.26;1001.32]	1.29 [0.76;2.21]
	Date(+30d)	0.97^{00} [0.79;1.19]	1.20^{0} [0.97;1.49]	$1.16^{*,0}$ [1;1.35]	0.99^{00} [0.82;1.21]	1.02 [0.64;1.61]	1.06^{00} [0.89;1.26]
Gcompo+Date	GB(+5m^2/ha)	$0.42^{***,-}$ [0.28;0.65]	$3.60^{***,++}$ [2.42;5.37]	0.68^{*} [0.49;0.96]	1.21 [0.8;1.82]	0.52 [0.16;1.7]	$0.53^{***,-}$ [0.37;0.76]
	GH(+5m^2/ha)	0.95^{00} [0.81;1.11]	1.18^{0} [0.89;1.57]	0.71^{***} [0.59;0.85]	1.35^{*} [1.08;1.7]	0.73 [0.41;1.31]	0.89^{0} [0.75;1.06]
	GO(+5m^2/ha)	$0.91^{*,00}$ [0.83;0.99]	1.04^{00} [0.86;1.25]	$0.80^{***,0}$ [0.74;0.87]	$1.25^{**,0}$ [1.07;1.46]	0.95^{0} [0.72;1.26]	1.02^{00} [0.93;1.12]
	Date(+30d)	1.10^{0} [0.92;1.3]	0.99^{00} [0.82;1.21]	1.07^{00} [0.9;1.27]	1.13^{0} [0.94;1.35]	0.90 [0.52;1.56]	$1.21^{*,0}$ [1.03;1.42]
AST+Date	AST (+10%)	$1.19^{*,0}$ [1.05;1.36]	$0.48^{**,-}$ [0.3;0.76]	$1.54^{***,+}$ [1.41;1.67]	$0.79^{*,0}$ [0.63;1]	1.28 [0.89;1.85]	1.00^{00} [0.86;1.16]
	Date(+30d)	1.07^{00} [0.90;1.28]	1.09^{0} [0.87;1.36]	0.96^{00} [0.82;1.12]	1.18^{0} [0.98;1.41]	0.93 [0.55;1.58]	$1.27^{**,0}$ [1.08;1.49]
Sand+Date	Sand(+11%)	1.00^{00} [0.85;1.18]	1.41^{**} [1.13;1.76]	1.03^{00} [0.86;1.24]	0.87^{0} [0.73;1.03]	0.69 [0.43;1.09]	1.02^{00} [0.89;1.18]
	Date(+30d)	1.11^{0} [0.93;1.33]	0.95^{0} [0.76;1.2]	1.08^{0} [0.88;1.32]	1.16^{0} [0.96;1.41]	1.05 [0.63;1.73]	$1.26^{**,0}$ [1.08;1.48]

The legend is the same as for Table 3.

Table 6.B

Multiplicative effect of a substantial variation in ecological variables with sampling date as additional variables on abundance of the second half species

Models	Variables	*Rubus fruticosus*	*Carex pilulifera*	*Deschampsia flexuosa*	*Festuca heterophylla*	*Holcus mollis*	*Teucrium scorodonia*
Age+Date	Age(+20 yr)	$0.82^{***,0}$ [0.73;0.92]	0.98^{00} [0.83;1.15]	$0.78^{***,0}$ [0.69;0.88]	$0.83^{***,0}$ [0.76;0.89]	$0.8^{**,0}$ [0.69;0.92]	$0.59^{***,-}$ [0.49;0.7]
	Date(+30d)	1.10^{0} [0.88;1.38]	1.10^{0} [0.82;1.48]	1.04^{0} [0.82;1.31]	1.05^{00} [0.9;1.22]	0.71^{*} [0.54;0.93]	1.31 [0.93;1.85]
STP+Date	STP_{CWS-SH}	2.03^{**} [1.21;3.4]	1.79 [0.94;3.42]	$3.74^{***,++}$ [2.31;6.04]	$2.10^{***,+}$ [1.44;3.04]	$3.72^{***,++}$ [2.09;6.63]	$10.13^{***,++}$ [4.53;22.62]
	STP_{SH-PH}	$1.54^{***,+}$ [1.40;1.62]	$0.52^{***,-}$ [0.25;0.64]	$0.48^{***,-}$ [0.29;0.75]	0.95^{0} [0.65;1.37]	$0.29^{***,--}$ [0.14;0.37]	$0.63^{***,-}$ [0.42;0.76]
	STP_{PH-MH}	$0.11^{***,--}$ [0.04;0.3]	0.83 [0.29;2.37]	0.70 [0.32;1.51]	0.61 [0.37;1.01]	1.71 [0.72;4.04]	0.25^{*} [0.07;0.89]
	STP_{MH-CWS}	3.06^{*} [1.13;8.33]	1.29 [0.52;3.23]	0.80 [0.4;1.59]	0.83 [0.53;1.3]	0.55 [0.3;1.02]	0.59 [0.16;2.18]
	Date(+30d)	0.87^{0} [0.68;1.1]	1.08^{0} [0.8;1.47]	1.05^{0} [0.81;1.38]	1.01^{00} [0.85;1.21]	0.78 [0.57;1.07]	1.15 [0.74;1.81]
Gcompo+Date	GB(+5m^2/ha)	0.68 [0.44;1.03]	1.07 [0.66;1.73]	$0.39^{***,-}$ [0.24;0.63]	$0.53^{***,-}$ [0.38;0.73]	0.48^{*} [0.27;0.84]	$0.22^{***,--}$ [0.1;0.47]
	GH(+5m^2/ha)	0.61^{***} [0.46;0.81]	0.53^{**} [0.36;0.78]	$0.55^{***,-}$ [0.43;0.71]	$0.74^{***,0}$ [0.62;0.88]	0.67^{**} [0.52;0.86]	$0.35^{***,--}$ [0.22;0.55]
	GO(+5m^2/ha)	1.02^{00} [0.91;1.14]	0.91^{00} [0.79;1.05]	$0.89^{*,00}$ [0.81;0.98]	1.03^{00} [0.95;1.12]	$0.81^{***,0}$ [0.72;0.91]	0.93^{00} [0.82;1.05]
	Date(+30d)	1.11^{0} [0.89;1.39]	1.03^{0} [0.78;1.36]	1.08^{0} [0.86;1.35]	1.06^{00} [0.91;1.23]	0.74^{*} [0.57;0.96]	1.45^{*} [1.01;2.07]
AST+Date	AST (+10%)	1.17^{0} [1;1.37]	1.16^{0} [0.93;1.44]	$1.47^{***,+}$ [1.3;1.67]	$1.16^{*,0}$ [1.03;1.32]	1.44^{***} [1.22;1.7]	$1.56^{***,+}$ [1.32;1.84]
	Date(+30d)	1.20^{0} [0.98;1.49]	1.08^{0} [0.82;1.44]	1.11^{0} [0.89;1.39]	1.14^{0} [0.97;1.34]	0.73^{*} [0.56;0.95]	1.58^{**} [1.13;2.21]
Sand+Date	Sand(+11%)	$0.75^{**,0}$ [0.63;0.89]	0.84^{0} [0.65;1.08]	0.95^{0} [0.77;1.18]	1.05^{00} [0.91;1.22]	1.25^{0} [0.99;1.59]	1.08^{0} [0.81;1.44]
	Date(+30d)	$1.29^{*,0}$ [1.06;1.58]	1.14^{0} [0.86;1.51]	1.21^{0} [0.96;1.53]	1.16^{0} [0.99;1.37]	0.82^{0} [0.63;1.07]	1.56^{**} [1.13;2.16]

The legend is the same as for Table 3.

Figure Captions

Fig. 1 Nested sampling design for dendrometry. We set up a 22-m-radius circular plot (A) and a 20 m × 20 m square plot nested within the 22-m-radius circular plot (B). Next, we divided the 20 m × 20 m plots into four smaller 10 m × 10 m quadrats and at the centre of each quadrat, we set up three circular plots with radii of 1, 2 and 4 m (C) (Chevalier, 2003)

Fig. 2 Sampling design to record skid trails in the 400 m^2 plots. In this putative example, the area of skid trail 1 and skid trail 2 within the 400 m^2 plot (in dark grey colour) was calculated and summed to represent the total skid trail area for the plot

Fig. 3 Relationship between stand type and skid trail area. SH: 34-year-old even-aged high forest, PH: 55-year-old even-aged high forest, MH: 104-year-old even-aged high forest, CWS: coppice-with-standards

Fig. 1

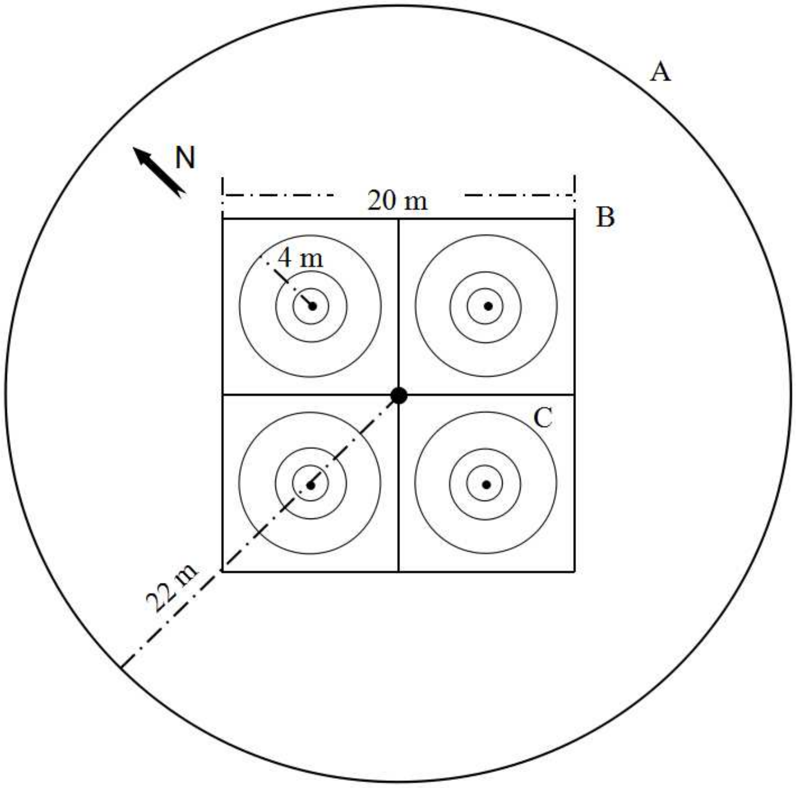


Fig. 2

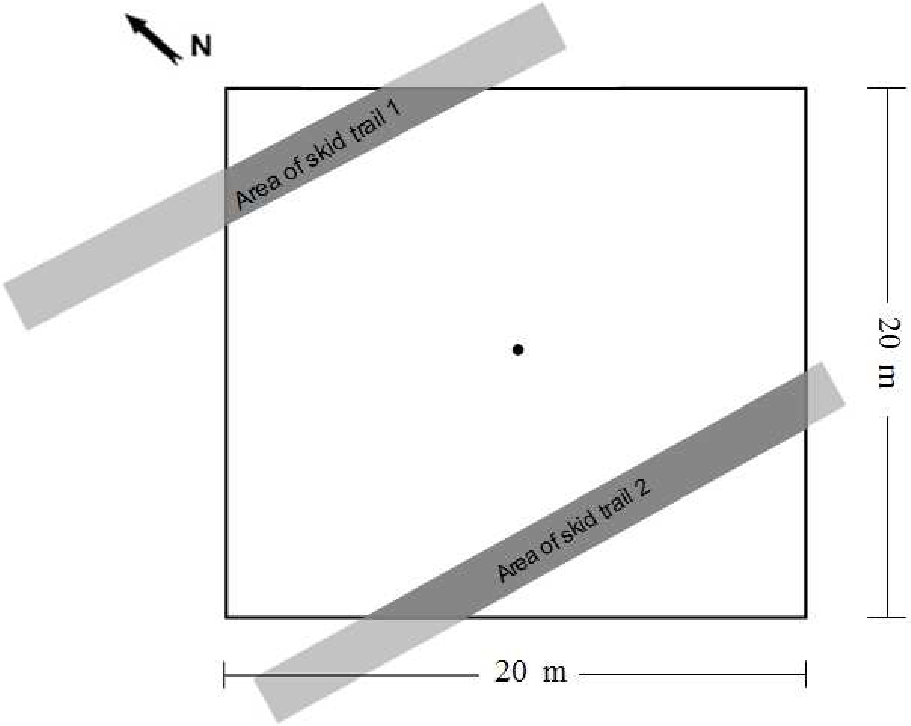
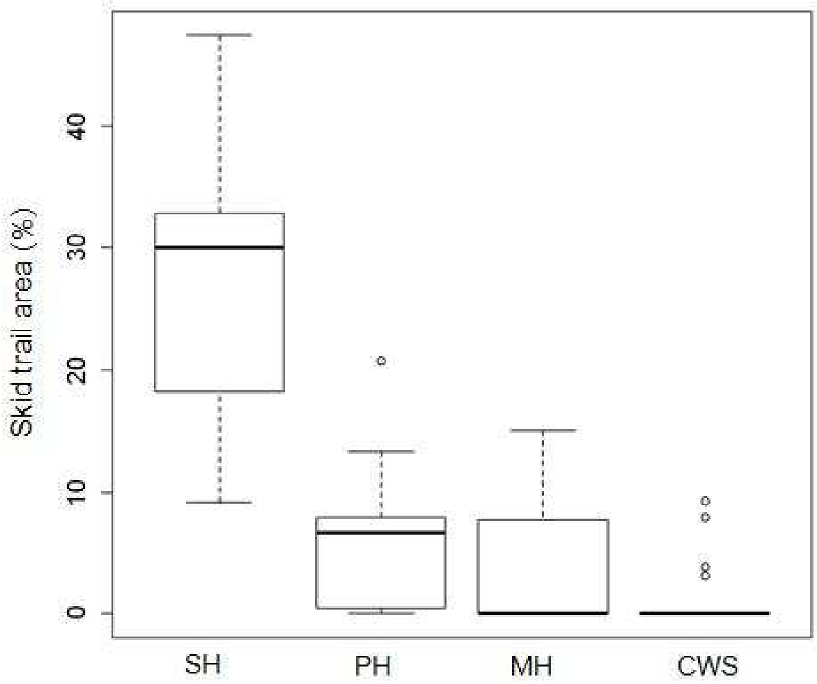


Fig. 3



Supplementary Material

Table SM 1

Different cases of describing negligibility effects of the variables

≥ 95% probability		effects
richness	abundance	
> 20%	> 50%	strongly positive
> 10%	> 25%	positive
[-20%; 20%]	[-50%; 50%]	weak
[-10%; 10%]	[-25%; 25%]	very weak
< 20%	< exp(0.5)	strongly negative
< 10%	< exp(0.25)	negative
-	-	uncertain

Table SM 2

Mean/Sd of species richness and abundance in different stand types and in plots with or without skid trails

		Stand type				Plots with/without skid trails	
		SH	PH	MH	CWS	with	without
Richness	Mean	37.5	26.33	12.67	15.68	28.03	15.75
	Sd	9.41	5.53	6.08	3.25	10.53	4.17
Abundance	Mean	205.2	125.19	62.73	74.85	140.32	76.48
	Sd	57.24	31.67	15.72	22.59	63.11	24.38

SH: 34-year-old even-aged high forest, PH: 55-year-old even-aged high forest, MH: 104-year-old even-aged high forest, CWS: coppice-with-standards

Table SM 3

Differences in QAICc values between the different ecological models and the null model (with sampling date as covariables in all models) for abundance of the ecological groups

	Woody species				Herbaceous species					
	SUCC		LIGHT		SUCC			LIGHT		
Models	MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age	-3.02	-16.16	-7.98	-6.42	-127.37	-42.53	-104.29	-101.01	-99.53	-32.44
Standtype	-4.68	**-33.52**	**-37.3**	-43.7	-147.75	-44.56	-124.11	-103.19	-120.2	-44.82
Gcompo	-10.1	-19.16	-7.71	-47.2	**-165.45**	**-56.68**	**-139.45**	**-113.78**	**-129.9**	**-46.02**
AST	**-14.8**	-11.08	0.839	**-50.8**	-108.34	-31.94	-77.16	-68.027	-111.5	-7.57
Sand	0.818	-14.27	-9.97	-0.40	-1.8076	-11.69	-15.24	1.8254	-2.11	-6.48

SUCC: succession status, LIGHT: light preference. MF: mature forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. The smaller the QAICc, the better the model with respect to the others. Within each ecological group, the model with the smallest QAICc is in bold.

Table SM 4

Multiplicative effect of a substantial variation in ecological variables on the abundance of the ecological groups

	Variables	Woody species				Herbaceous species					
		SUCC		LIGHT		SUCC			LIGHT		
		MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age+Date	Age(+20yr)	$0.95^{*,00}$ [0.91;1]	$0.80^{***,0}$ [0.72;0.89]	$0.89^{**,00}$ [0.83;0.96]	$0.92^{*,00}$ [0.86;0.99]	$0.6^{***,-}$ [0.54;0.67]	$0.76^{***,0}$ [0.69;0.83]	$0.66^{***,-}$ [0.6;0.74]	$0.53^{***,-}$ [0.45;0.62]	$0.70^{***,-0}$ [0.65;0.76]	0.69^{***} [0.6;0.8]
	Date(+30d)	$1.08^{*,00}$ [1.00;1.17]	1.06^{0} [0.86;1.31]	1.13^{0} [0.98;1.29]	1.02^{00} [0.89;1.16]	1.09^{0} [0.87;1.36]	0.80 *,0 [0.67;0.95]	$0.78^{*,0}$ [0.64;0.96]	1.18^{0} [0.87;1.61]	0.96^{00} [0.82;1.13]	0.73^{*} [0.56;0.96]
STP+Date	STP$_{CWS-SH}$	$1.35^{**,+}$ [1.11;1.64]	$2.52^{***,++}$ [1.62;3.92]	1.30 [0.95;1.78]	$2.02^{***,++}$ [1.58;2.57]	$8.94^{***,++}$ [5.85;13.67]	$3.92^{***,++}$ [2.72;5.63]	$5.41^{***,++}$ [3.74;7.81]	$13.91^{***,++}$ [7.02;27.57]	$5.02^{***,++}$ [3.76;6.68]	$4.09^{***,++}$ [2.32;7.23]
	STP$_{SH-PH}$	0.81^{0} [0.66;1.00]	1.00^{0} [0.66;1.53]	1.62^{**} [1.18;2.21]	$0.37^{***,--}$ [0.28;0.5]	$0.41^{***,--}$ [0.29;0.59]	$0.41^{***,--}$ [0.28;0.6]	0.56^{***} [0.4;0.78]	$0.46^{**,-}$ [0.29;0.75]	$0.40^{***,--}$ [0.3;0.53]	1.00 [0.62;1.63]
	STP$_{PH-MH}$	0.84^{0} [0.65;1.10]	$0.11^{***,--}$ [0.04;0.31]	$0.20^{***,--}$ [0.12;0.33]	1.53^{*} [1.04;2.24]	$0.25^{**,--}$ [0.11;0.58]	0.94 [0.55;1.61]	$0.14^{***,--}$ [0.07;0.3]	$0.16^{**,-}$ [0.04;0.61]	0.55^{*} [0.34;0.91]	$0.04^{***,--}$ [0.01;0.17]
	STP$_{MH-CWS}$	1.08^{0} [0.86;1.37]	$3.58^{*,+}$ [1.34;9.57]	$2.43^{***,+}$ [1.48;3.98]	0.88^{0} [0.64;1.2]	1.09 [0.48;2.45]	0.67 [0.43;1.04]	2.30^{*} [1.15;4.62]	0.98 [0.26;3.77]	0.91 [0.58;1.42]	$6.68^{*,+}$ [1.54;28.96]
	Date(+30d)	1.08^{00} [0.99;1.17]	0.89^{0} [0.71;1.1]	0.96^{00} [0.84;1.09]	1.11^{00} [0.98;1.25]	1.04^{0} [0.81;1.35]	0.85^{0} [0.69;1.03]	0.68^{***} [0.55;0.84]	1.07^{0} [0.71;1.6]	0.99^{00} [0.84;1.17]	$0.55^{***,-}$ [0.41;0.75]
GB+Date	GB(+5m2/ha)	0.88^{0} [0.76;1.02]	0.61^{*} [0.41;0.91]	0.71^{*} [0.53;0.93]	0.91^{0} [0.74;1.11]	$0.29^{***,--}$ [0.19;0.45]	$0.42^{***,--}$ [0.3;0.59]	$0.14^{***,--}$ [0.09;0.24]	$0.14^{***,--}$ [0.06;0.3]	$0.39^{***,--}$ [0.29;0.54]	$0.08^{***,--}$ [0.03;0.2]
	GH(+5m2/ha)	$0.90^{**,00}$ [0.83;0.97]	$0.59^{***,-}$ [0.46;0.76]	$0.82^{*,0}$ [0.7;0.96]	$0.80^{***,0}$ [0.71;0.89]	$0.36^{***,--}$ [0.27;0.47]	$0.63^{***,-}$ [0.54;0.74]	0.69^{***} [0.59;0.81]	$0.35^{***,--}$ [0.24;0.51]	$0.56^{***,-}$ [0.47;0.65]	0.81^{0} [0.64;1.02]
	GO(+5m2/ha)	$0.93^{**,00}$ [0.89;0.97]	0.95^{00} [0.86;1.05]	1.04^{00} [0.96;1.13]	$0.82^{***,0}$ [0.78;0.87]	$0.84^{***,0}$ [0.78;0.9]	$0.86^{***,00}$ [0.8;0.92]	$0.90^{**,00}$ [0.83;0.96]	$0.85^{**,0}$ [0.78;0.94]	$0.84^{***,00}$ [0.79;0.89]	1.03^{00} [0.91;1.15]
	Date(+30d)	$1.11^{**,00}$ [1.03;1.20]	1.10^{0} [0.90;1.35]	1.13^{0} [0.99;1.3]	1.08^{00} [0.97;1.2]	$1.31^{*,0}$ [1.06;1.62]	0.86^{0} [0.74;1.01]	0.86^{0} [0.72;1.02]	1.46^{*} [1.06;2.01]	1.10^{0} [0.95;1.28]	0.72^{*} [0.55;0.94]
AST+Date	AST (+10%)	$1.13^{***,00}$ [1.07;1.20]	$1.29^{***,0}$ [1.13;1.47]	1.07^{00} [0.95;1.19]	$1.33^{***,0}$ [1.24;1.42]	$1.67^{***,+}$ [1.5;1.85]	$1.44^{***,+0}$ [1.3;1.59]	$1.51^{***,+}$ [1.36;1.68]	$1.72^{***,+}$ [1.5;1.96]	$1.56^{***,+}$ [1.44;1.68]	$1.30^{**,0}$ [1.09;1.54]
	Date(+30d)	$1.09^{*,00}$ [1.01;1.17]	1.16^{0} [0.95;1.4]	$1.19^{*,0}$ [1.04;1.36]	1.00^{00} [0.9;1.11]	1.33^{*} [1.06;1.66]	0.87^{0} [0.74;1.03]	0.93^{0} [0.77;1.12]	1.5^{**} [1.12;2.03]	1.09^{00} [0.94;1.26]	0.89^{0} [0.69;1.14]
Sand+Date	Sand (+11%)	1.04^{00} [0.97;1.11]	$0.72^{***,0}$ [0.61;0.84]	$0.82^{***,0}$ [0.73;0.91]	1.07^{00} [0.95;1.21]	0.87^{0} [0.69;1.11]	1.17^{0} [0.99;1.38]	$0.79^{*,0}$ [0.65;0.95]	0.95^{0} [0.72;1.26]	0.89^{0} [0.75;1.07]	0.76^{*} [0.61;0.94]
	Date(+30d)	$1.11^{*,00}$ [1.03;1.20]	$1.27^{*,0}$ [1.06;1.53]	$1.24^{**,0}$ [1.09;1.41]	1.06^{00} [0.93;1.21]	1.43^{*} [1.08;1.87]	0.96^{00} [0.8;1.15]	1.08^{0} [0.87;1.33]	1.53^{*} [1.11;2.12]	1.21^{0} [0.99;1.48]	0.99^{0} [0.78;1.26]

Variations were: an addition of 20 years for high forest age, 5 m^2 ha^{-1} for basal area data (G_B, G_H, G_O), 10% for skid trail area (AST), 11% for sand content (Sand), 30d for sampling date (Date) and a transition from sapling to pole stage in even-aged forests ($STP_{SH\text{-}PH}$), pole to mature stage in even-aged forests ($STP_{PH\text{-}MH}$) and mature even-aged forest to coppice-with-standards stands ($STP_{MH\text{-}CWS}$). Levels of statistical significance of parameters are symbolized as follows: ***$p<0.001$, **$p<0.01$, *$p<0.05$. ‘‘0’’ and ‘‘00’’ indicate that the effect has a *p*-value of at least 0.975 of being negligible at two different levels. ‘‘$^{-}$’’ and ‘‘–’’ indicate that the effect has a *p*-value of at least 0.975 of being negative and non-negligible at two different levels. ‘‘$^{+}$’’ and ‘‘$^{++}$’’ indicate that the effect has a *p*-value of at least 0.975 of being positive and non-negligible at two different levels (further details are given in the Data analysis section). Values in brackets are 97.5% confidence intervals of the coefficients.

Table SM 5

Multiplicative effect of the variables of the best model with skid trails on the abundance of the ecological groups

Variables	Woody species				Herbaceous species					
	SUCC		LIGHT		SUCC			LIGHT		
	MF	PF	INT	HEL	MF	PF	NF	SHA	INT	HEL
Age(+20 yr)										
STP$_{CWS-SH}$		1.38 [0.59;3.23]	1.04 [0.58;1.89]							
STP$_{SH-PH}$		1.64 [0.79;3.40]	1.93^{*} [1.15;3.26]							
STP$_{PH-MH}$		$0.11^{***,--}$ [0.04;0.31]	$0.20^{***,--}$ [0.12;0.33]							
STP$_{MH-CWS}$		$3.83^{**,+}$ [1.45;10.17]	$2.49^{***,+}$ [1.52;4.09]							
G$_{B}$(+5m^2/ha)	0.95^{00} [0.79;1.13]			1.13^{0} [0.89;1.44]	$0.32^{***,--}$ [0.2;0.51]	$0.45^{***,-}$ [0.3;0.66]	$0.17^{***,--}$ [0.1;0.29]	$0.15^{***,--}$ [0.07;0.34]	$0.48^{***,-}$ [0.35;0.67]	$0.08^{***,--}$ [0.03;0.22]
G$_{H}$(+5m^2/ha)	0.95^{00} [0.85;1.06]			0.93^{00} [0.81;1.07]	$0.38^{***,--}$ [0.28;0.52]	0.66^{***} [0.53;0.81]	$0.78^{*,0}$ [0.64;0.95]	$0.37^{***,--}$ [0.24;0.57]	0.65^{***} [0.54;0.78]	0.83^{0} [0.61;1.12]
G$_{O}$(+5m^2/ha)	0.96^{00} [0.9;1.02]			$0.90^{**,00}$ [0.83;0.97]	$0.87^{**,00}$ [0.78;0.96]	$0.88^{*,00}$ [0.79;0.97]	0.96^{00} [0.87;1.07]	0.89^{0} [0.77;1.02]	$0.91^{*,00}$ [0.84;0.99]	1.04^{00} [0.88;1.23]
AST (+10%)	1.25 [0.93;1.67]	1.92 [0.9;4.08]	1.28 [0.73;2.22]	1.85^{**} [1.28;2.68]	1.26 [0.76;2.09]	1.18 [0.71;1.97]	1.62 [1.00;2.62]	1.26 [0.65;2.45]	1.74^{**} [1.17;2.59]	1.11 [0.49;2.51]
Sand(+11%)										
Date(+30d)	$1.03^{*,00}$ [1.01;1.06]	0.96^{00} [0.89;1.03]	0.98^{00} [0.94;1.03]	1.01^{00} [0.98;1.05]	$1.09^{*,00}$ [1.01;1.17]	0.95^{00} [0.9;1]	$0.94^{*,00}$ [0.88;1]	$1.13^{*,00}$ [1.01;1.26]	1.02^{00} [0.97;1.07]	$0.89^{*,00}$ [0.81;0.98]

The legend is the same as for Table SM 4.

Table SM 6.A

Multiplicative effect of the variables of the best model with skid trails on abundance of the first half species

Variables	*Carpinus betulus*	*Fagus sylvatica*	*Quercus petraea*	*Hedera helix*	*Ilex aquifolium*	*Lonicera periclymenum*
Age(+20 yr)						
STP_{CWS-SH}			1.46 [0.87;2.44]	0.18 *,- [0.05;0.73]	2.23 [0.32;15.55]	1.66 [0.76;3.62]
STP_{SH-PH}			$0.30^{***,--}$ [0.17;0.5]	$7.53^{**,++}$ [2.15;26.33]	0.12 [0.01;1.02]	1.29 [0.65;2.57]
STP_{PH-MH}			$2.87^{***,++}$ [1.80;4.58]	$0.27^{**,-}$ [0.12;0.60]	0.24 [0.00;18.5]	$0.37^{**,-}$ [0.21;0.66]
STP_{MH-CWS}			0.81 [0.57;1.15]	2.72^{*} [1.26;5.85]	15.7 [0.25;975.53]	1.25 [0.73;2.15]
GB(+5m^2/ha)	$0.40^{***,-}$ [0.25;0.65]	$2.47^{**,+}$ [1.46;4.15]				
GH(+5m^2/ha)	0.91^{0} [0.73;1.14]	0.90 [0.61;1.32]				
GO(+5m^2/ha)	0.89^{0} [0.77;1.01]	0.90^{0} [0.71;1.14]				
AST (+10%)	0.86 [0.44;1.68]	0.18^{*} [0.04;0.8]	1.28 [0.90;2.69]	1.69 [0.53;5.35]	0.82 [0.11;6.03]	0.71 [0.33;1.53]
Sand(+11%)						
Date(+30d)	1.03^{00} [0.97;1.1]	1.01^{00} [0.95;1.08]	1.04^{00} [1;1.09]	0.99^{00} [0.93;1.06]	1.01^{00} [0.86;1.17]	1.02^{00} [0.97;1.08]

The legend is the same as for Table SM 7.A.

Table SM 6.B

Multiplicative effect of the variables of the best model with skid trails on abundance of the second species

Variables	*Rubus fruticosus*	*Carex pilulifera*	*Deschampsia flexuosa*	*Festuca heterophylla*	*Holcus mollis*	*Teucrium scorodonia*
Age(+20 yr)						
$STP_{CWS\text{-}SH}$	1.43 [0.54;3.77]					
$STP_{SH\text{-}PH}$	2.02 [0.88;4.63]					
$STP_{PH\text{-}MH}$	$0.11^{***,--}$ [0.04;0.31]					
$STP_{MH\text{-}CWS}$	3.19^{*} [1.17;8.71]					
GB(+5m^2/ha)		0.87 [0.47;1.59]	0.46^{**} [0.27;0.78]	0.54^{**} [0.37;0.79]	0.46^{*} [0.24;0.86]	$0.23^{***,--}$ [0.1;0.53]
GH(+5m^2/ha)		$0.45^{**,-}$ [0.27;0.73]	0.62^{**} [0.46;0.85]	0.76^{*} [0.6;0.94]	0.64^{*} [0.46;0.89]	$0.36^{***,-}$ [0.21;0.62]
GO(+5m^2/ha)		0.83^{0} [0.67;1.03]	0.95^{00} [0.83;1.09]	1.05^{00} [0.93;1.18]	$0.79^{*,0}$ [0.66;0.94]	0.95^{00} [0.79;1.14]
AST (+10%)	1.47 [0.61;3.53]	0.52 [0.16;1.66]	1.55 [0.80;3.01]	1.09 [0.62;1.90]	0.86 [0.35;2.11]	1.18 [0.50;2.77]
Sand(+11%)						
Date(+30d)	0.95^{00} [0.88;1.03]	1.02^{00} [0.93;1.12]	1.02^{00} [0.94;1.10]	1.02^{00} [0.96;1.07]	$0.91^{*,00}$ [0.83;0.99]	1.13^{00} [1.00;1.27]

The legend is the same as for Table SM 7.A.

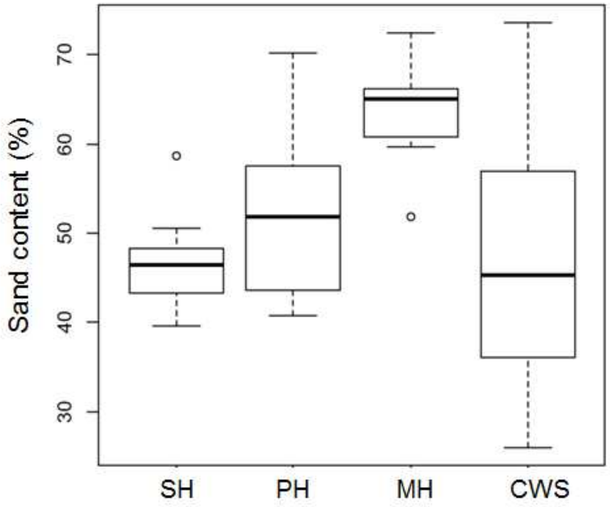


Fig. SM 1 Distribution of sand content depending on stand type. SH: 34-year-old even-aged high forest, PH: 55-year-old even-aged high forest, MH: 104-year-old even-aged high forest, CWS: coppice-with-standards.

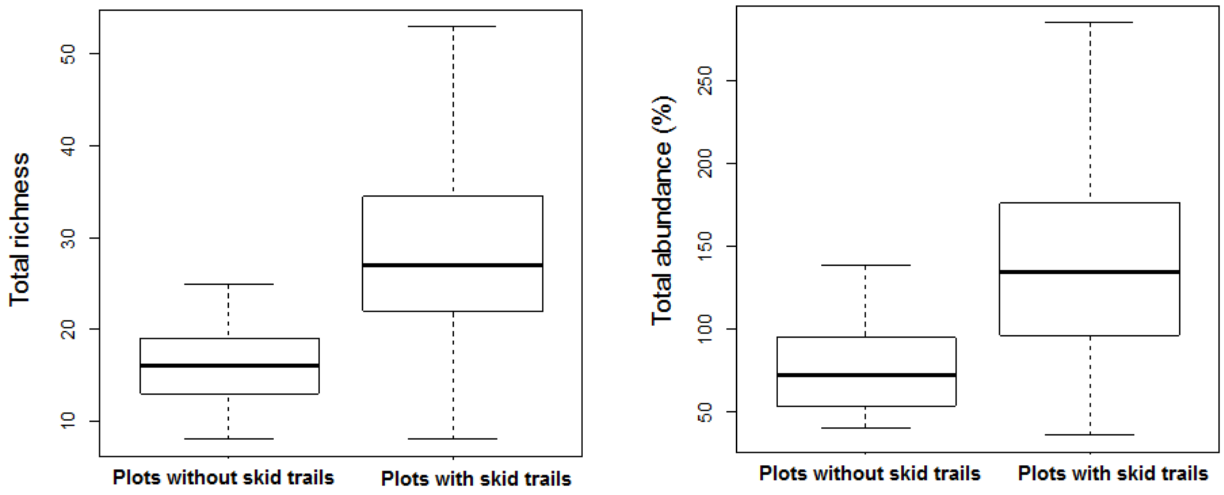


Fig. SM 2 Distribution of total richness/total abundance on plots with and without skid trails

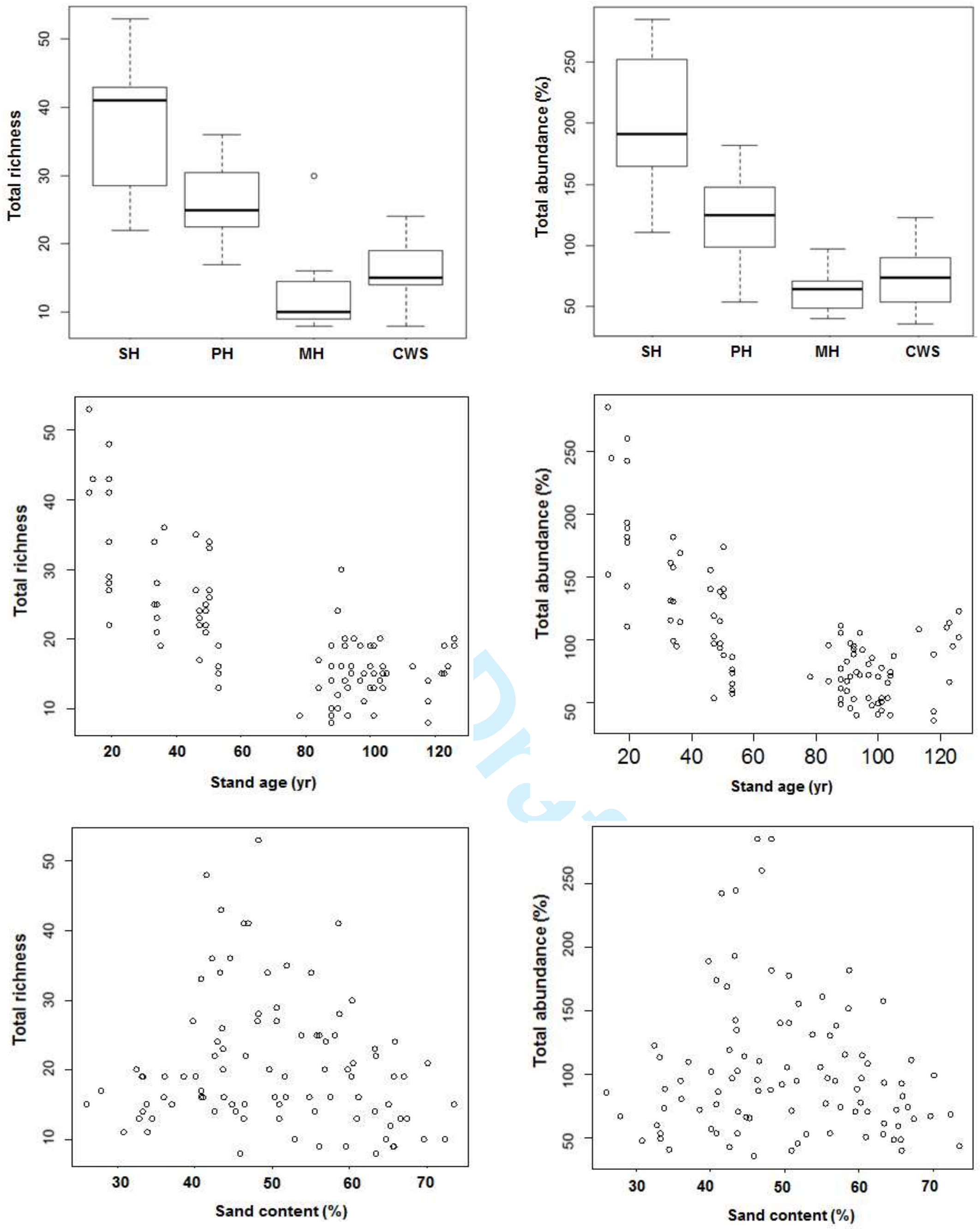


Fig. SM 3 Relationship between total richness/total abundance and stand type, stand age or stand content. SH: 34-year-old even-aged high forest, PH: 55-year-old even-aged high forest, MH: 104-year-old even-aged high forest, CWS: coppice-with-standards.