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Impacts des caractéristiques du peuplement et des cloisonnements sur la biodiversité floristique en forêt de plaine

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Chapter I Introduction

1.1 European temperate forest management, mechanisation and ground flora diversity

Maintaining or improving biodiversity is an important goal of sustainable forest management (Lindenmayer et al., 2000; Ministerial Conference on the Protection of Forests in Europe, 2011). The temperate regions are among the zones of the world that have been most uniformly, extensively modified by human activities since very long times, which have often resulted in dramatic impacts on biological diversity (Franklin, 1988). European temperate forests today are the result of centuries of human activities (Spiecker et al., 2003). Large areas of forests in the temperate zone have been converted to agricultural land, and former forest area has been used for buildings, roads and other land uses (Spiecker et al., 2003). Temperate forests in Europe cover a large bioclimatological range from oceanic to continental forests, and from floodplain to mountain forests up to the alpine timberline. Forests are often located close to farmland or in densely populated urban areas, being managed for the production of roundwood (Hagner, 1999; Reich and Frelich, 200;). They also increasingly provide ecological services (e.g. water supply, stream water quality, carbon storage), ecological benefits (wildlife, biodiversity) and human values (recreation, tourism, aesthetics, spirituality) (Reich and Frelich, 2002). Ellenberg (1986) stated that current tree species composition of temperate forests in Europe is mainly determined by former past land use and management rather than by natural factors. Though during the last decades forest cover has increased steadily (0.37% per year) in Europe (Forest Europe and UNECE FAO, 2011), forest harvesting intensity (the ratio of harvested timber volume and net annual increment volume) also increased from 58% in 1990 to 62.4% in 2010 and is expected to increase further (UNECE and FAO, 2011; Böttcher et al., 2012; Christian Levers et al., 2014). With the burgeoning global populations, the future extent, composition, health, and productivity of temperate forest may well signal whether human civilization at high population density is compatible with the sustainability of ecological health and productivity (Reich and Frelich, 2002).

Nowadays, most forest harvesting is highly mechanized in temperate forests (Ampoorter, 2011). Mechanized forest harvesting started at the beginning of the 20th century, when tractors were brought into action in forest stands for the removal of logs or complete trees. By the 1950s, specialized forestry machines such as harvesters, forwarders, skidders, feller bunchers and knuckleboom loaders were introduced into forests for felling and logging (Acker et al., 2004; Ampoorter, 2011). Mechanized ground-based logging machines are widely used since they generally provide a safer work environment, higher quality end products, and greater labor productivity (Akay et al., 2007). Yet, modern heavy equipment, such as bulldozers and skidders, produces a most serious soil compaction (Whitman et al., 1997; Pinard et al., 2000; Fredericksen and Pariona, 2002) in comparison with other anthropogenic activities, such as shifting cultivation, forest fires, and trampling (Alegre and Cassel, 1996; Rab, 1996; Talbot et al., 2003). Greater use of heavy logging equipment and the development of special skidding equipment have growing potential for forest site damage. Despite the careful planning of the related field operations, concern remains over the potential adverse impacts to the forest ecosystem, especially on sensitive forest sites (Nugent et al., 2003).

In view of the challenge of how future management can cope with the objectives of maintaining biodiversity, a more ecologically oriented approach of forest management should be emphasized (Spiecker et al., 2003; Rykowski et al., 1999). Ground flora in temperate forests, which has the highest floristic species diversity of all forest layers, plays an important role in forest ecosystems with respect to revegetation, productivity, aesthetics, wildlife habitat, and water and nutrient cycling. (Metzger and Schultz, 1984; Thomas et al., 1999; Gilliam, 2002; Zenner and Berger, 2008). Gilliam et al., (2007) demonstrated that the herbaceous layer represents less than 1% of the biomass of the forest, yet can contain 90% or more of the plant species of the forest. Furthermore, ground flora is particularly sensitive to a variety of factors such as overstory characteristics (Nagaike, 2002; Augustoet al., 2003; Nagaike et al., 2005; Barbier et al., 2008), soil properties (Brunet et al., 1996), forest disturbances or management practices (Hammond and Miller, 1998; Wender et al., 1999). Therefore, the diversity of ground flora is also an important indicator to help to evaluate forest site quality and the environmental impact of management (Pregitzer and Barnes, 1982; Gilliam, 2002). Not all species were demonstrated to be equally affected by forestry, some species are often little or even positively affected (Bengtsson et al., 2000). However, species with narrow requirements for habitat conditions may be more sensitive to disturbances. The more intense disturbances may exclude these species for a long period of time (Gilliam et al., 2007).

1.2 Skid trails

1.2.1 Role of skid trails in managed forests

In managed forests, machinery timber harvesting relies on forest roads, and even more on parallel skid trails perpendicular to the roads (Avon, et al., 2010, 2013). Skid trails provide easy access from roads to stand interiors. The forest products are generally transported from stump to the landing areas by rubber-tired skidders or crawler tractors (Decocq et al., 2004; Akay et al., 2007; Ebrecht and Schmidt, 2008; Veldman and Putz, 2010). In addition, skid trails are often evenly distributed across the stands and this is especially the case in lowland managed forests where management is likely to be intense (Avon et al 2013). The networks of skid and tractor trails are integral features of managed stands and landscapes, and have microsite conditions and plant communities that differ from the surrounding patches of forest without forest floor and soil disturbance (Buckley et al., 2003).

The skid trail system is a visible system of machinery disturbance (Heninger et al., 2002). It has the advantage of confining the disturbances to relatively smaller areas (Akbarimehr and Jalilvand, 2013). On the one hand, the length, width and of skid trails will affect the area of disturbance in addition to the number of trees felled (Duah-Gyamfi et al 2014); on the other hand, machine wheels often create continuous ruts which function as preferential paths for runoff during rainfall. The depth of the ruts can indicate the vertical disturbance on soil (Jansson and Johansson, 1998; Page-Dumroese et al., 2010; Picchio et al., 2012). In addition, skid trails can indicate not only the extent of soil disturbance but also the overstory and understory disturbance over the trails. The overstory cover above skid trails were also measured in previous studies as an indicator of cutting intensity (Zenner and Berger, 2008). In fact, the total skid trail area at landscape scale has been used as an indicator of management activities or intensity in previous studies. For example, Garland (1997) demonstrated that a goal of less than 15 % of the harvest area in skid trails, including landings but excluding haul roads, is considered reasonable for skid trail planning.

1.2.2 Effects of skid trails on soil properties

Machine passes on skid trails have an important influence on soil structural characteristics, soil aeration and the soil water balance, and may therefore considerably affect chemical and physical properties of soil and cause damages to natural tree regeneration (Najafi et al., 2009; Akbarimehr and Jalilvand, 2013). Detrimental soil disturbance on forest soil, associated with ground-based harvesting, often includes rutting, lateral soil displacement, horizon mixing, and compaction (Clayton et al., 1987; Reeves et al., 2012).

Soil is compacted when forces exceed soil resistance (Schafer et al., 1989). Soil compaction following skidder traffic, a leading cause of soil degradation (Brais, 2001), has been shown to cause changes in soil structure (Akbarimehr and Naghdi, 2012), to reduce porosity (Gent et al., 1984), to increase bulk density (Akay et al., 2007; Lotfalian and Bahmani, 2011) and water runoff (Najafiet al., 2009) thereby inducing soil erosion (Jusoff, 1996) and influence plant regeneration (Bassett et al., 2005) and growth (Snider and Miller, 1985; Lotfalian and Bahmani, 2011; Lorente et al., 2012). The initial passes cause the highest increase in soil compaction in relation to subsequent passes but these may lead to further soil disturbance by deepening the ruts (Schack-Kirchner et al., 2007; Najafi et al., 2008). Deep continuous ruts often occur when traffic is applied to soil. Ruts may also function as preferential channels for superficial water flow and thus cause erosion since the infiltration of rainwater is reduced (Startsev and McNabb, 2000). Such ruts are able to persist for years (Najafi et al., 2008). At the most severely compacted sites, including skid trails and log landings, in dipterocarp forests in Malaysia the compaction degree of soils are 2–4.5 times higher than at undisturbed locations (Jusoff, 1991; Mohd and Ang, 1991; Hattori et al, 2013). Gracen and Sands (1980) report that the skidding of logs affects the soil to a depth of 0.30 m.

Assessing the persistence of soil compaction effects over time is an integral part of the assessment of forest harvesting impacts (Croke et al., 2001). The recovery process of compacted soil may take several decades or even centuries. Hattori et al., (2013) found that soil compaction was still apparent more than 20 years after a dipterocarp forest had been logged-over. Bulk densities remained significantly higher in tracks and landings 17–23 years after timber harvesting in wet forests of South-Eastern Australia (Pennington and Laffan, 2004). Shallow soil compaction was detected in the Amazon forest 16 years after harvesting operations (McNabb et al., 1997). Under cool temperate conditions, the consequences of soil disturbance by traffic of harvest machinery can persist for decades in clay loam to silt loam soils and soil profiles below wheel tracks may require 70 to 140 years to recover (Froehlich et al., 1985; Webb et al., 1986; Ezzati et al., 2012). Quantifying the recovery of on-site impacts of soil compaction is important for determining potential cumulative impacts over time (Croke et al., 2001).

1.2.3 Effects of soil compaction on plant

Soil compaction has been shown to influence the regeneration, growth, diversity, proliferation, and recovery of the forest ground flora (Mou et al., 1993; Roberts and Gilliam, 1995; McCarthy et al., 2001; Buckley et al., 2003; Berger et al., 2004;

Godefroid and Koedam, 2004; Zenner and Berger, 2008). Soil compaction due to skidding may prevent the establishment of seedlings from seeds whose dormancy was broken by the gap microclimate. Removal of topsoil during skidding will also displace the seeds stored in it (Pinard et al., 1996; Duah-Gyamfi et al 2014). Greacen and Sands (1980) and Heilman (1981) reported that the elongation rate and penetration of primary roots are reduced when soil is compacted, inducing a lower uptake of nutrients and water (Kozlowski, 1999; Jordanet et al., 2003). Compaction consequently leads to reduced tree growth (Gebauer and Martinkova, 2005) and a higher tree seedling mortality (Brais, 2001; Stone and Kabzems, 2002; Maynard and Senyk, 2004; Hattori et al., 2013). Godefroid and Koedam (2004) investigated the interspecific variation in soil compaction sensitivity among forest floor species, and found that the cover of 65 species (61%) was significantly related to soil compaction. Twenty four forest species (58% of all forest species tested) showed significant growth responses to soil compaction. A few, such as *Carex strigosa*, *Epilobium montanum* and *Mycelis muralis*, showed monotonic reduction in growth with increasing compaction, but about half showed a bell-like response with maximum growth at 200 N (*Hyacinthoides non-scripta*) or 400 N (e.g., *Carex pilulifera*, *Melica uniflora*) or even 600 N (*Oreopteris limbosperma*). Small and McCarthy (2002) studied the response of eastern deciduous forest herbs to experimental light and soil compaction treatments. They found that soil compaction caused severe reductions in height and biomass of *Eupatorium rugosum* and *Osmorhiza claytonii*, which are early- and late-successional species respectively. Hence, understanding the long-term effects of harvest trail compaction and scarification on forest floor nutrient availability, microbial dynamics and competing vegetation is important for elucidating the influence of machinery harvesting on long-term ecosystem resilience, functioning and biodiversity maintenance (Lorente et al., 2012).

1.2.4 Soil compaction sampling

Soil compaction is regarded as one of the criteria representing the effect of a mechanical force on soils (Özgöz et al., 2006). The degree of compaction and the depth of compacted layers can vary across the area of interest. The accurate and rapid determination of soil compaction properties is essential for ecologists and forest managers (Özgöz et al., 2006). Jones and Kunze (2004) summarized the following key issues that influence both the measurement and treatment of compaction: 1) Intensity – How compacted is the soil relative to uncompacted soils? Slight compaction may not cause management problems and may heal over time. 2) Extent – Is the compaction across the entire training/disturbed area or concentrated in specific areas? 3) Depth – At what depth does the highest compaction occur? 4) Seasonality – How, if at all, does compaction change over the course of a year?

To characterise soil compaction, bulk density, penetration resistance, hydraulic conductivity, and porosity are mainly used. Soil compaction increases bulk density and penetration resistance (Ngunjiri & Siemens, 1995; Abu-Hamdeh et al., 2000), and decreases porosity (Abu-Hamdeh et al., 2000; Gysi et al., 2000), hydraulic conductivity (Arvidsson 2001), and infiltration rates (Abu-Hamdeh et al., 2000; Van Dijck & Van Asch 2002; Özgöz et al., 2006). Studies on compaction have mainly focused on a few properties such as bulk density, penetration resistance, and hydraulic conductivity, rather than more time-consuming pore-size distribution (Özgöz et al., 2006).

Soil bulk density (D_b) is the ratio of mass of dry soil to bulk volume of soil. Bulk density expressed as Mg/m^3, is commonly used to measure soil compaction. The-mass of soil sample is determined after drying to constant weight at 105 ℃, and bulk volume is determined by a sampling core, cylinder or excavation. An increase in D_b

indicates that movement of air and water within the soil has been reduced; the soil therefore may be more likely to erode or be less favorable for plant growth (Miller et al., 2001). Yet, higher density of gravel or stones in soils complicates bulk density measurement. Also, it is hard to make comparisons of bulk density between soils or horizons with differing amounts of coarse mineral or organic fragments. The real density of these fragments differs from that of the bulk density of the fine soil (< 2 mm), whole-soil bulk density will invariably be greater when gravel is present. Although equipment for bulk density sampling is relatively inexpensive and durable for field usage, the assessment of bulk density is time consuming. Furthermore, Miller et al., (2001) stated that little is known about the relative accuracy (precision plus bias) and efficiency (cost per unit of precision) of various bulk density samplers.

Cone penetrometers are also commonly used to measure soil compaction because of their easy, rapid operation (Perumpral, 1987; Bengough & Mullins, 1990). Cone penetrometer is a device forced into the soil to measure its resistance to vertical penetration (Miller et al., 2001). However, cone penetrometer readings can be strongly dependent on soil moisture content, which limits their use and interpretation (Busscher, 1990; Miller et al., 2001). Field sampling for comparative purposes should be done when soils are near field capacity to minimize the influence of soil moisture on the sampling accuracy (Miller et al., 2001).

1.2.5 Effects of skid trails on plants

The creation and periodic use of skid trails cause changes in stand structure – for example, by opening up the canopy – and stand structure is very important in determining the biodiversity in forests (Price, 1998). Stand structure creates heterogeneity and complexity, and houses a variety of organisms. Harvesting methods, silvicultural systems, and stand-tending practices that retain or lead to recruitment of structural attributes make ecological sense (Lertzman et al., 1997). 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 (Jonsson and Esseen, 1990; Hansen et al, 1991; Price, 1998). 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 very important that forest managers understand their influence on ground flora diversity at stand scale. Structural attributes of forest stands are increasingly recognized as being of theoretical and practical importance in understanding and managing forest ecosystems because: stand structure is the attribute most often manipulated to achieve management objectives following establishment of a forest stand; structure is a readily measured surrogate for functions (e.g. productivity) or for organisms (e.g. cavity-dwelling animals) that are difficult to measure directly; structures have direct value as a product (e.g. wood) or in providing a service (e.g. in sequestering carbon or influencing hydrologic responses) (Franklin et al., 2002).

Micro-site environment on skid trails differs from than in interior forest. Previous studies have reported higher canopy opening, soil compaction, soil nutrient loss and soil moisture on skid trails compared to undisturbed habitat (Buckley et al., 2003; Hattori et al., 2003; Zenner and Berger, 2008). These environmental changes might explain the differences of ground flora observed between the locations on and off skid trails (Harvey and Brais, 2002; Swaine and Agyeman, 2008; Wolf, 2008; Avon et al., 2013). In particular, skid trails as sources and corridors for dispersal can play an important role in the introduction of nonnative plants into stands (Milberg and

Lamont 1995; Trombulak and Frissell, 2000; Gelbard and Belnap, 2003; Nelson, et al 2014).

Canopy cover is one of the most important factors that control a site's microclimate (Metzger and Schultz, 1984). Opening canopy on skid trails can influence plant growth and competition patterns, especially between shade tolerant and intolerant species (Horn, 1971; Planchais and Sinoquet, 1998). However, light level may not always stay high on skid trails years after logging or cutting operations. The duration of canopy closure together with residual tree stands properties (age, height...) can largely regulate light availability on skid trails.

Soil compaction is one of the major consequences of mechanized harvesting on skid trails (Najafi et al., 2009; Ampoorter et al, 2010; Naghdi et al., 2010; Solgi and Najafi, 2014). Though multiple studies have demonstrated soil compaction effect on plant, very few studies so far directly related ground flora to soil compaction measured from skid trails. Therefore, the role of compaction on skid trails is still a hypothesis to be validated. For instance, Buckley et al., (2003) measured soil compaction degree as a description of the growth conditions on skid trails, but did not directly link it to ground flora diversity in the statistical analyses. Some studies investigated the effects of soil compaction (penetration resistance or bulk density) in the area covered by skid trails on ground flora, however, their investigation were at large quadrat scale (100 m^2 or 60 m^2 plots) (Hattori et al., 2013; Zenner and Berger, 2008; Berger et al., 2004). In fact, we found only two studies investigating the relationship between soil compaction on skid trails and ground flora at small scale. Yet, their results were not consistent. Roovers et al., (2004) demonstrated that the intensity of soil compaction was highly correlated with species cover (negatively) and composition. On the contrary, Heninger et al., (2002) found that reduced Douglas-fir tree seedling height on skid trails was unrelated to percentage increases in soil bulk density. Since the recovery process of soil compaction may take several decades or even centuries (; Greacen and Sands, 1980; Croke et al., 2001; Godefroid and Koedam, 2004), and could vary a lot at local scale, we assumed that it might also be an important soil property affecting the regeneration and growth of ground flora.

Soil moisture is an important fine-scale factor affecting plant in many studies (Beckage et al., 2008; Beckage et al., 2000; Gray et al., 2012) but those dealing with skid trails did not find consistent results. For example, some studies demonstrated that soil moisture was higher on skid trails due to the removal of canopy cover that reduced rainfall intercept and increased water intercept in the soil, while some others found decreased water holding ability on wheel rut after the first machine passes (Miller and Sirois, 1986; Buckely, et al., 2003; Solgi and Najafi, 2004; Ezzati et al., 2012). Since the influence of canopy cover and machine use on soil moisture have not been jointly compared in a study, soil moisture level on skid trials and its relation to canopy cover and soil disturbance still need to be tested.

Studies have demonstrated the effects of skid trails on plant regeneration, growth and diversity. Particularly, tree regeneration and growth on skid trails compared to undisturbed habitat were often studied. Yet, results were not consistent: skid trails may enhance, have no effect or reduce on subsequent tree growth. For example, Harvey and Brais (2002) found that higher disturbance levels in skid trails favored the establishment of larch (*Larix laricina (Du Roi) K. Koch*), raspberry (*Rubus idaeus L.*), and graminoids. Reduction of ericaceous cover occurred in skid trails on coarse-textured sites but was only temporary. Significantly higher postlogging recruitment of timber tree species was also shown in felling gaps and skid trails than in areas unaffected by logging (Swaine and Agyeman, 2008). But Liechty et al., (2002) showed that compaction on skid trails frequently elevated bulk density to levels that could reduce regeneration success or seedling growth (Liechty et al., 2002).

Concerning the plant diversity affected by skid trails, nonnative, ruderal or non-forest species were often found to be significantly less abundant in treated stands than on skid trails (Nelson et al., 2008; Avon, 2013; Godefroid and Koedam, 2004). Skid trails had a greater percentage of wetland species (9%) than in forest, but differences in richness between skid trails and forest were not statistically significant (Buckley et al., 2003). Myrmecochorous, barochorous and epizoochorous species, as well as species with short light seeds occurred more often on skid trails. Godefroid and Koedam (2004) concluded that the presence of a path resulted in an increase in the number of ruderal and nitrogen-demanding species, as well as indicator of disturbance and of basic soil conditions.

1.2.6 Skid trail disturbance among different stand types

Diversity pattern of ground flora influenced by management disturbance (e.g. harvesting method and intensity) might vary among stand types. Gilliam et al., (1995) assessed the effects of forest management practice-clear-cutting on plant biodiversity in a mid-Appalachian hardwood forest, and found a correlation between herbaceous layer and the overstory in mature stands (>70 year following selective cutting) but not in young stands (20 year following clear-cutting). Zenner et al., (2007) emphasized that potentially adverse effects of soil disturbances from skidding traffic on regeneration, growth responses, and soil recovery may be of particular concern for forest types that are managed on short rotations or managed with silvicultural systems that require repeated harvesting entries.

Similarly, for skid trails effects on ground flora diversity, limited studies systematically compared their effects among stand types (Roovers et al., 2004; Swaine 2008). Soil compaction degree on skid trails might be different among stand types. Several studies have demonstrated that in forests with single-tree or group selection harvests, bulk density on primary skid trails was significantly greater than in undisturbed areas. Whereas in forests with shelterwood harvesting or clearcuts, bulk density on skid trails was not significantly different from that in undisturbed areas (Kluender et al., 1994; Stokes et al., 1993; Turton et al., 1997; Liechty et al 2002). Furthermore, trees at different ages may intercept different levels of light and water. The different combinations of soil compaction level, light availability, soil moisture and other ecological factors could ultimately result in significant variation in ground flora diversity pattern. Therefore, skid trails effects on ground flora might differ among tree stand types.

1.3 The effects of tree stand on ground flora diversity

In managed forests, the choice of tree species is one of the forester's fundamental acts. Tree species richness and dominance is considered as a biodiversity indicator (MCPFE, 2003; Barbier et al., 2008). Forest age influences the chemical and structural properties of soil, and consequently affects understory vegetation (Honnay et al., 1999; Dupouey et al., 2002). Tree abundance (represented by basal area, stem density) is shown in numerical studies to have negative effect on understory vegetation diversity (Alaback and Herman, 1988; Thomas et al., 1999). The preservation or absence of a subcanopy layer greatly modifies understory vegetation, especially by modifying understory light (Kwiatkowska, 1994; Nagaike et al., 1999). Tree species composition also influences ground flora diversity, though the results are inconsistent. For example, in comparison of understory diversity in coniferous trees with deciduous trees, there were 10 results with higher understory richness under hardwoods and 4 results with higher SR under conifers (Barbier et al., 2008). Besides, fewer studies compared hardwood (or coniferous) species internally.

It is difficult to make generalizations on the effect of tree species on understory diversity, the effects of tree species on ground flora diversity vary greatly and some results are even conflicting (Barbier et al., 2008). This may be partly due to other factors not taken into account in most studies, especially those related to site characteristics and management practices (Barbier et al., 2008). More precise indications on past land use (especially former agricultural land or forest land), forest history (tree age and past tree composition), tree regeneration method (natural or plantation, e.g. Fahy and Gormally, 1998), thinning intensity in the last decades (e.g. Nagaike, 2002) would be useful for clarifying how a tree species acts through specific management practices (Barbier et al., 2008). Given that silviculture and the growth of overstory can profoundly affect the composition and development of understory species (Alaback and Herman 1988; Stewart 1988; Bailey et al., 1998; Thomas et al., 1999), it is important to understand what the relationships between overstory and undertory species are and, more importantly, how silviculture regimes would affect these relationships (He, 1999).

1.4 Study of biodiversity at different spatial scales

Multiple studies have mandated that successful conservation planning must account for the effects of spatial scaling of species diversity (e.g., Margules et al., 1988; Gaston et al., 2001). Our understanding of scale-dependent patterns of biodiversity, however, is incomplete. Even in well-studied temperate-forest ecosystems, our insufficient knowledge of spatial variation in species diversity and composition is an impediment to the conservation of biodiversity and sustainable resource management (Ehrlich 1996; Summerville et al., 2001). Furthermore, most temperate-forest ecosystems are poorly protected in reserves or are managed for timber production (e.g., Norton 1996). Investigation on skid trail disturbance at different scales can provide information on which scale is most critical for determining species composition and persistence (Summerville et al., 2003).

At different scales, different sets of mutually reinforcing ecological processes leave their imprint on spatial, temporal and morphological patterns (Peterson et al., 1998). For example, ground flora at stand scale is typically dominated by processes that operate relatively uniformly over the entire stand (Franklin et al., 2002). At fine scale, the combination of soil disturbance, compaction and of an altered light availability that accompanies skidding traffic could bring about a diversity change in the herb layer (Small and McCarthy, 2002; Decocq et al., 2004; Godefroid and Koedam, 2004), in particular in favor of non-forest species (Buckley et al., 2003; Ebrecht and Schmidt, 2003, 2005; Ampoorter et al., 2007).

Chapter II Research objectives

2.1 General research objective

Our general research objective was to detect the effects of stand attributes and skid trails on ground flora diversity at two spatial scales - stand scale and fine scale. Though the effects of tree stand attributes or skid trails have been studied in previous studies, no study compared their respective roles on ground flora diversity. Furthermore, knowledge is lacking on the variation of skid trail effects on ground flora among stand types.

To represent the stand scale, plot size was 400 m^2 for vegetation sampling and up to 1300 m^2 for large tree sampling. Generally, the vegetation and soil within each plot had the same management history and had been subjected to similar disturbances.

The specific objectives of the study are detailed below.

2.2 What are the respective single and combined effects of tree stand attributes and skid trail area on understory diversity at stand scale?

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; Brosofske et al., 2001; Emmer et al., 1998). For example, when comparing understory vascular plant diversity in hard wood stands with those in deciduous 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 (e.g. management practices), which may positively or negatively influence the effects of tree stand attributes on ground flora, have not been identified or disentangled before reaching conclusions (Barbier et al., 2008).

Skid trail system might be as important as stand attributes in contributing to inconsistent results (Barbier et al., 2008; He and Barclay, 2000). However, no study ever included skid trail effects in the study of tree stand attributes. 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). Yet, 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 stand scale.

Therefore, the primary objective of this thesis was to assess the respective single and combined effects of tree stand attributes and skid trail area on understory diversity at stand scale. In order to embrace all types of stands for better understanding the potential influence of skid trail effects, 96 oak-dominated stands including even-aged high-forest (29, 55 or 104 years old) and standard-with-coppice stands were selected in the Montargis forest.

2.3 What is the relative importance of subplot location, soil moisture, soil compaction light and stand type on ground flora diversity at fine scale?

Fine-scale studies of diversity pattern can provide insights into how historical and environmental filters interact across scales to influence vegetation locally (Leibold et al., 2004; Burton et al., 2011). No study ever compared the influence of skid trail disturbance and micro-environmental factors on ground flora diversity at fine scale.

Micro-site environment on skid trails might differ from interior forest, such as canopy opening, higher soil compaction, soil nutrient loss or increased soil moisture on skid trails compared to undisturbed habitat (Buckley et al., 2003; Hattori et al., 2003; Zenner and Berger, 2008) (For more details were in the section 1.2.5 of Introduction)

The relative importance of different environmental or history filters (e.g. disturbance) for ground flora diversity may vary with forest stage or development (Burton et al., 2011). Limited researches compared the diversity pattern on skid trails in different forest types. Roovers et al., (2004) examined the effects of trampling skid trails on vegetation along trails in four vegetation types: two deciduous forest types, one grassland and one heathland, and showed that the increase in floristic dissimilarity from trail to undisturbed vegetation was higher in forests than in grassland and healthland, whereas no difference was detected between the two forests types. Liechty et al., (2002) and Beaudet (2014) proved that regeneration failures occurred on skid trails in stands harvested using single-tree selection but not in stands with shelterwoods or clearcuts. Swaine (2008) investigated timber tree regeneration on skid trails in two forest reserves in first and second rotations respectively. However, these studies were not enough informative for drawing conclusions on the exact role skid trails played in different forests.

Therefore, our study intended to investigate fine-scale understory diversity pattern in three high forest stand types of varying tree maturity with skid trail system, as well as to find out the dominant factors affecting ground flora diversity among subplot location, soil moisture, soil compaction, light, stand type and basal area. For subplot location, we used subplots on and off skid trails to indirectly represent habitat exposed to frequent and infrequent disturbances. In addition, within skid trails, we used different types of location - middle of skid trails, wheel track and edge of skid trails - to represent the disturbance gradient within skid trails.

2.4 Are the dominant factors affecting the ground flora diversity different among ecological groups and among individual species?

The classification of the ground flora into ecological groups is a basic and important step to better document biodiversity responses. Relationships between ecological or functional groupings of plant species and environmental gradients can provide evidence for environmental filtering, particularly when the traits suggest an advantage in the associated environment (McGill et al., 2006; Burton et al., 2011)**.**

In this study, we hypothesized that the response of ground flora to the ecological variables can be affected by the species traits as follows: life form, seed bank strategy, light and moisture requirements and successional status (data source: Julve, 2007; Hodgson et al., 1995). Tree regeneration on skid trails was often investigated in previous studies. Seed bank was considered to be an important potential seed source for the restoration of plant communities (Bakker & Berendse 1999), which has been shown to be related to the ground vegetation response to skid trails (Roovers et al., 2004; Godefroid and Koedam, 2004). Light and moisture requirements as well as successional status are also basic plant traits widely used in studies of ground flora diversity (Brockerhoff et al., 2003; Jennife et al., 2005; Fierke and Boone Kauffman, 2005).

2.5 Is the influence of skid trails different at stand scale and at fine scale?

It is useful to understand the different role of skid trails at two scales, which could provide useful information for skid trail design and forest management such as: a) at stand scale, distinguish the sensitive stand to skid trail system, and estimate the appropriate area or density for different stand types; b) at local scale, find out the suitable width, spacing of skid trails under different types of forest. In addition, it could help identify the scale that was most affected by skid trail disturbance.

Chapter III Individual and combined effects of tree stand attributes and skid trail area on ground flora diversity at stand scale

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3.1 Abstract

Previous studies investigating the relationship between tree stand attributes and ground flora have neglected the potential influence of skid trails at stand scale. Yet, stands with different characteristics may be subjected to varying intensities of machinery use and may have differing skid trail area. Our study assessed the effects of tree stand attributes (age, stand type, basal area) and skid trail area on ground flora diversity at 400 m^2-plot scale in Montargis forest in the northern half of France. The richness and abundance of ecological groups were calculated based on the classification of their successional status and light preference. We analyzed Generalized Linear models through model comparison tools and assessed the magnitude of the effects of each variable. The results were: at ecological group level, model comparisons indicated that among-plot floristic variations were mostly associated to stand type or tree species basal area, depending on the successional traits or light preference of the species group. Although we found non-negligible effects of skid trail area on ground flora except for forest species, the effects of skid trail area disappeared when tree stand attribute effects were incorporated into the statistical model. At species level, only one species had a non-negligible response to skid trails, about 70% of the investigated 29 species (occurrence >25%) showed neither non-negligible nor negligible responses. Considering that mechanisation is commonly used in current forest management, stronger effects might be expected in the long-term.

3.2 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 (Thomas et al., 1999), plays multiple important roles in biodiversity (Gilliam, 2002; He and Barclay, 2000). Furthermore, due to its sensitivity to a variety of factors such as overstory characteristics (Augusto et al., 2003; Barbier et al., 2008; Nagaike, 2002; Nagaike et al., 2005), soil properties (Brunet et al., 1996), forest disturbances or management practices (Hammond and Miller, 1998; Wender et al., 1999), ground flora diversity is also an important indicator to help to evaluate forest site quality and the environmental impact of management (Gilliam, 2002; Pregitzer and Barnes, 1982).

Many choices made by forest managers influence ground flora. One of the forester's most fundamental acts is the selection of tree species (Barbier et al., 2008). Tree composition and abundance influence micro environments and resource availability (Barbier et al., 2008; Binkley and Giardina, 1998; Duguid and Ashton, 2013; Jennings et al., 1999; Kirby and Watkins, 1998). Indeed, canopy light transmittance can be affected by the properties of tree species such as the spatial arrangement of leaves (Horn, 1971; Planchais and Sinoquet, 1998) or leaf size (Barkman, 1992). Soil water availability is affected by trees through differing amounts of non-intercepted water or quantity of water absorbed by tree roots (Barbier et al., 2008 and 2009). Trees can also largely influence nutrient recycling by changing the rates of soil organic matter decomposition and nutrient mineralization (Prescott, 2002). As a result, changes in tree composition and abundance can induce changes in understory growth and mortality (Augspurger, 1984; Burton & Mueller-Dombois, 1984) and modify the competitive interactions between species, especially between shade tolerant and shade intolerant species. This will in turn induce changes in forest floor species composition and diversity (Metzger & Schultz, 1984; Uresk and Severson, 1989; Sibbald et al., 1991). 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; Brosofske et al., 2001; Emmer et al., 1998). For example, when comparing understory vascular plant diversity in hard wood stands with those in deciduous 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 tree 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; He and

Barclay, 2000). Indeed, how the stand is regenerated, stem density and cutting frequency are dependent on tree species.

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). The creation and periodic use of skid trails cause changes in stand structure – for example, by reducing structural legacy or opening up the canopy – and stand structure is very important in determining the biodiversity in forests (Price, 1998). 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; Jonsson and Esseen, 1990; Price, 1998). 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 their influence on ground flora diversity at stand scale. Another issue is soil compaction, which causes changes in soil structure (Akbarimehr and Naghdi, 2012), reduces porosity (Gent et al., 1984), increases bulk density (Akay et al., 2007; Lotfalian and Bahmani, 2011) and water runoff (Najafi et al., 2009) thereby inducing soil erosion (Jusoff, 1996), and ultimately influences plant regeneration (Bassett et al., 2005) and growth (Lorente et al., 2012; Lotfalian and Bahmani, 2011; Snider and Miller, 1985). The degree of compaction is much higher on skid trails than in undisturbed areas and the recovery process may take several decades or even centuries (Croke et al., 2001; Godefroid and Koedam, 2004; Greacen and Sands, 1980). Hence, skid trails may play an important role in shaping 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 stand scale. Moreover, it has been indicated by Baltzinger et al., (2011) that at stand scale (400 m^2) skid trails and tractor rut may contribute to a significant part of the variation of floristic richness.

Our study intended to investigate the effects of tree stand attributes and skid trail area on ground flora diversity at stand scale. In our study, to represent the stand scale, plot size was 400 m^2 for vegetation sampling and up to 1300 m^2 for large tree sampling. Generally, the vegetation and soil within each plot had the same management history and had been subjected to similar disturbances. Species with similar environmental affinities or which grow in similar conditions are likely to have consistent responses to similar disturbances (Pregitzer et al., 2001; Simpson et al., 1990; but see for example Godefroid et al., 2005 for contrary results). 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. Previous studies have confirmed more shade-intolerant and non-forest species along skid trails (Buckley et al., 2003; Fredericksen and Mostacedo, 2000; Godefroid and Koedam, 2004; Zenner and Berger, 2008). We therefore retained light demand and successional status as two important plant species traits which may be involved in floral response to skid trails. According to the study by Godefroid and Koedam (2004), the abundance of 61% of the species was significantly related to soil compaction. We therefore assumed that individual species might also show significant responses to the effects of skid trails at stand scale. Three questions were asked: (1) What are the respective single and combined effects of tree stand attributes and skid trails on understory diversity? (2) Does light preference and successional status determine the direction and magnitude of the ground flora response? (3) Are there strong combined effects of tree stand attributes and skid trails on the abundance of individual species?

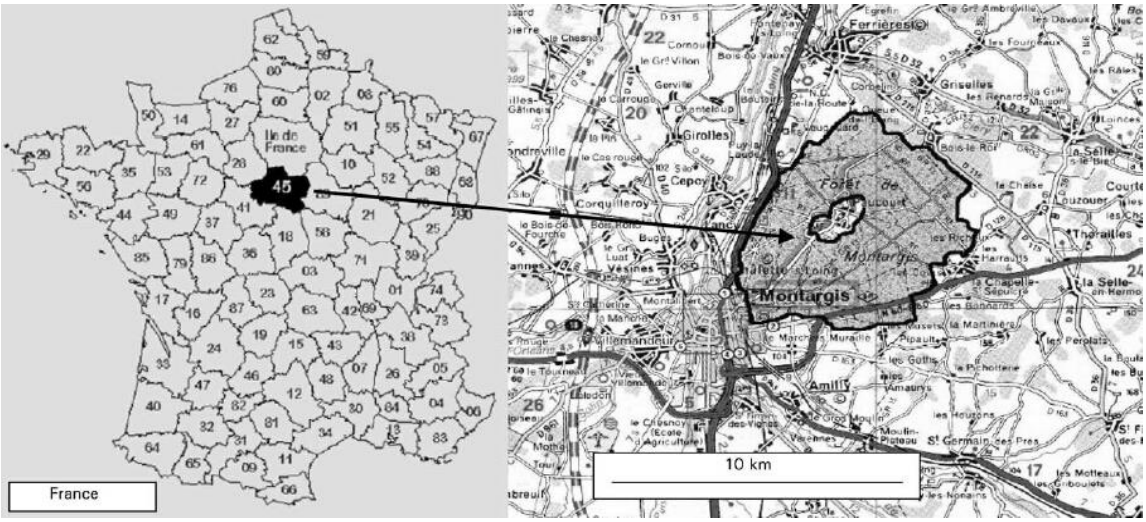

Figure 3.1 Location map of the Montargis forest (Jean-Franc and Richard, 2006).

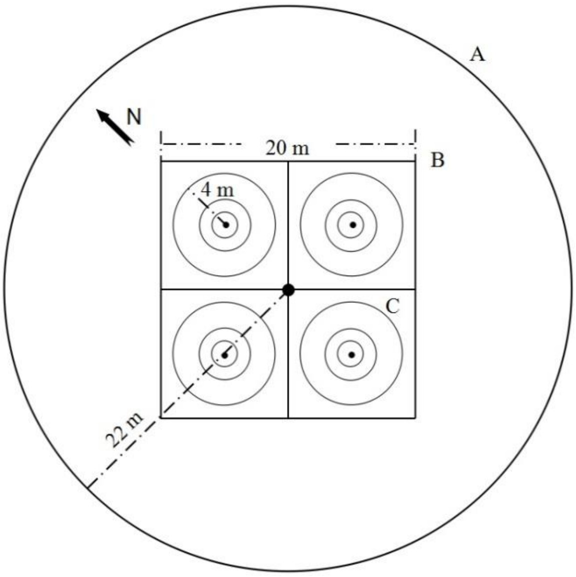

Figure 3.2 Nested sampling design for dendrometry. We set up a 22-m-radius circular plot (A) and a 20 m × 20 m square plot nested within the 22-m-radius circular plot (B). Next, we divided the 20 m × 20 m plots into four smaller 10 m × 10 m quadrats and at the centre of each quadrat, set up three circular plots with radii of 1, 2 and 4 m (C) (Chevalier, 2003).

3.3 Materials and methods

3.3.1 Study area

The Montargis forest (48°01' N, 2°48' E, Loiret, France) is an ancient state forest managed by the French National Forestry Office (ONF), which covers 4090 ha and is located in the northern half of France (Fig. 3.1). 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 variegated 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 standard-with-coppice (SWC) system with sessile oak as standards and hornbeam as coppice, though the area has partly been converted to an even-aged high forest since 1857. The current SWC stands are gradually being converted to regular high-forest stands (by progressively homogenising diameter classes), while the existing regular high-forest stands have already undergone the typical seed-tree/natural regeneration phase of the system.

3.3.2 Data collection

Data collection was done in 2000 by one of the authors (Richard Chevalier). Ninety-six stands representing four forest types (three different even-aged high forest types and one SWC forest type) were selected (cf. Table 3.1). 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 stronger in mature high stands (64%) than in the other stand types (46 to 55%). In each stand, we set up a 22-m-radius circular plot and a 20 m × 20 m square plot nested within the

22-m-radius circular plot (Chevalier, 2003). Next, 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. 3.2).

We then proceeded to measure the diameter at breast height (“DBH”, in cm) for each tree, and recorded their diameter classes, which were defined as follows: class 0: 0.5 m ? height < 1.3 m, class 1: Height ? 1.3 m and DBH < 2.5 cm, class 5: 2.5 cm ? DBH < 7.5 cm, class 10: 7.5 cm ? DBH < 12.5 cm, class 15: 12.5 cm ? DBH < 17.5 cm, class 20: 17.5 cm ? DBH < 22.5 cm…Tree classes were recorded in the different plots: (1) class ? 20 trees in the 22-m-radius circle; (2) class 10 and class 15 trees in the four 10 m-×-10 m quadrats; (3) class 5 trees in the four 4-m-radius circles; (4) class 1 trees in the four 2-m-radius circles; (5) class 0 trees in the four 1-m-radius circles.

Vegetation was sampled once in each plot 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. Finally, our main focus was on ecological groups other than the vernal group. In each 20 m × 20 m square plot, all plants below 2 m in height were recorded following the Braun-Blanquet abundance-dominance classification: i: one unique individual, cover < 5%; +: very few individuals, total cover < 5%; 1: few to many individuals, total cover < 5%; 2: total cover [5; 25%[; 3: total cover [25; 50%[; 4: total cover [50; 75%[; 5: 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. 3.3), 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.

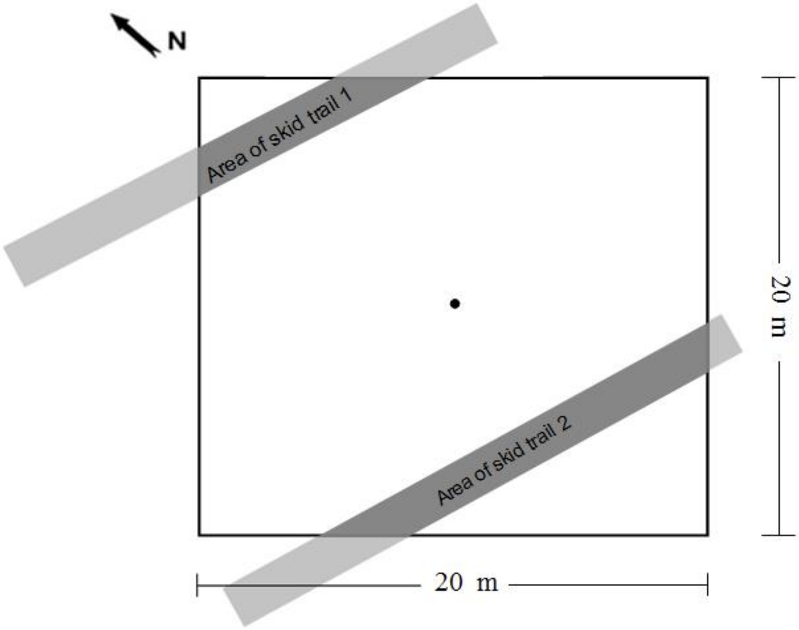

Figure 3.3 Sampling design to record skid trails in the 400 m^2 plots. In this putative example, the area of skid trail 1 and skid trail 2 within the 400 m^2 plot (in dark grey colour) was calculated and summed to represent the total skid trail area for the plot.

Table 3.1 Statistical summary of the ecological variables used in the models

Variable	Description	Mean	SD
Age	High-forest stand age (year or class)	71.83	33.77
STP	Stand type (4 types): 3 even-aged high forest (HF) types: SH: 34 years old, PH: 55 years old, MH: 104 years old; and 1 standard-with-coppice (SWC) type	---	---
G	Total stand basal area at breast height of total tree stands (m^2/ha)	24.24	7.31
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^{-1})	G_O:18.02 G_B:1.91 G_H:4.31	G_O:7.29 G_B:2.21 G_H:4.51
AST	Relative area of skid trails within plot (%) (Fig. 3.3)	AST of SH: 15.83 AST of PH: 16.33 AST of MH: 6.25 AST of SWC: 2.30	AST of SH: 7.54 AST of PH: 12.76 AST of MH: 10.17 AST of SWC: 7.05

3.3.3 Data analysis

We analyzed the effects of the variables related to tree stand attributes and skid trails (Table 3.1) on ground flora diversity at the 400-m^2 scale. Both richness and abundance of ground flora were calculated, based on a species classification by successional status and light preference. The abundance-dominance coefficients (i, +, 1, 2, 3, 4 and 5) were transformed into the following respective cover percentages: 0.1%, 0.5%, 5%, 17.5%, 37.5%, 62.5% and 87.5%. For successional status, we classified the species into three groups following Julve (2002) as in Barbier et al., (2009): (i) forest species (MF) whose preferred habitat is mature forests, (ii) peri-forest species (PF) whose habitats are found close to mature forests either temporally (in the early stages of succession) or spatially (along edges), and (iii) non-forest species (NF) whose preferred habitats are not linked to forests. We also distinguished three groups according to light preference (Ellenberg indicator value L, Ellenberg et al., 1992): shade-tolerant ($L < 5$, SHA); intermediate light ($5 \leq L < 7$, INT), and heliophilous ($L \geq 7$, HEL) (Table SM. 3.8).

We analysed the magnitude and negligibility of the effect of each variable on each of the six ecological groups. We first calculated the magnitude of the effects of each variable (single-variable models listed in Table 3.1) and kept the best single model (ie. with the smallest QAICc value), then added the skid trails as additional variables to analyze the magnitude of their combined effects on the ecological group diversity. The statistical models were Quasi-poisson generalized linear models (glm) for coefficient estimation (Wedderburn, 1974; McCullagh, 1983) and Poisson glm for the model comparison with QAICc with a common dispersion parameter for all the models being compared (because species counts could not be strictly assumed to follow a Poisson distribution and QAICc cannot be calculated for Quasi-poisson models) (Table 3.2 and 3.3). The link function was the default (log) for these models. The common dispersion parameter was taken to be that of the Quasi-Poisson Gcompo model (see below for a definition of this model). We calculated the multiplicative coefficient of the mean fitted value for species richness (Table 3.4) and abundance data (Table 3.5), to estimate the response of ground flora – in multiplicative terms due to the log link function – to the numerical increase in tree stand attributes and skid trails. Here, the multiplicative coefficient was calculated with an increase in the variables of about one standard deviation (cf. Table 3.1): 20 years increment for age, 5 m^2 ha^{-1} for basal area, and 5% for skid trail area (Tables 3.4-3.7). For stand type (STP), we calculated the associated multiplicative coefficient by supposing the stand changed from one type to the next successive type: sapling to pole stage in even-aged stands ($STP_{SH\text{-}PH}$), pole to mature stage in even-aged stands ($STP_{PH\text{-}MH}$) and mature even-aged forest to standard-with-coppice stands ($STP_{MH\text{-}SWC}$). We reported the mean value of the multiplier for each variable, its 95% confidence interval (Tables 3.4-3.7) and the *P*-value (Tables SM.3.1-3.4 in Supplementary Material).

Analyses based only on *P*-values are unable to distinguish different situations in 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 this test whether the trend is ecologically important. The important question is actually whether the true trend is ecologically negligible or not (Dixon and Pechmann, 2005). As Dixon and Pechmann (2005) and Barbier et al., (2009) did, we distinguished strong (b_1) and weak (b_2) negligibility intervals for both richness and abundance data ($0 < b_1 < b_2$) to define two equivalence regions that include all values of the trend parameters that are ecologically negligible (strongly negligible for b_1 and weakly for b_2). In our analysis we chose $b_1 = 0.1$, $b_2 = 0.2$ for species richness, and $b_1 = 0.25$, $b_2 = 0.5$ for abundance as in Barbier et al., (2009). That is, we considered that a change of 10% in species richness (or 25% in abundance) was a weak change, while a change of 20% (or 50% in abundance) was a strong change. Three different cases occur when describing negligibility effects: (1) negligible effects: “0” when the value of the multiplier (denoted by β) follows $P(-b_2 < \log(\beta) < b_2) \geq 0.95$ and “00” for the more stringent: $P(-b_1 < \log(\beta) < b_1) \geq 0.95$; (2) non-negligible negative effects: “-” for $P(\log(\beta) < -b_1) \geq 0.95$ and “−” for the stronger: $P(\log(\beta) < -b_2) \geq 0.95$; (3) non-negligible positive effects: “+” for $P(\log(\beta) > b_1) \geq 0.95$ and “++” for the stronger: $P(\log(\beta) > b_2) \geq 0.95$ (Tables 3.4-3.7).

For the above ecological groups, to determine whether there are any effects of skid trails on species composition other than abundance or 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.

Since sand content was the only site type variable that had strong variations among stand types, we checked whether the inclusion of sand content in the best model for each ecological group significantly changed the conclusions (Table SM. 3.5 in Supplementary Material).

To detect whether there were strong effects of skid trails on species abundance at species level, we made model comparison for each of the species that occurred in more than 25% of the plots (29 species were selected from the total 159 species) (Table SM. 3.6 in Supplementary Material). The magnitude and negligibility of the combined effects of the best indicative variables and skid trails were also calculated (Table SM. 3.7 in Supplementary Material).

3.4 Results

Single variable models

Models related to stand type (STP) were the best models for the overall richness of the ecological groups combined and for the abundance of peri-forest (PF), shade-tolerant (SHA) and intermediate groups (INT), while basal area by tree species (Gcompo) was the best predictor of abundance for forest (MF), non-forest (NF) and heliophilous species (HEL). The QAICc values of the models associated to skid trail area were the lowest, except for two groups whose QAICc values were higher than that of the models related to stand age (e.g. the abundance of MF and PF) and for two groups for which skid trail area were the best indicator (PF, HEL) (Tables 3.2 and 3.3).

Table 3.2 Differences in QAICc values between the different ecological models and the null model for richness of the ecological groups (see also Table 3.1)

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age	-73.70	-47.65	-107.99	-71.75	-68.96	-102.94
STP	-81.29	-73.57	-120.58	-79.95	-103.58	-120.26
Gcompo	-69.67	-56.74	-103.44	-69.30	-88.06	-101.43
AST	-44.23	-76.38	-55.88	-45.68	-51.35	-72.46

MF: 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 underlined.

Table 3.3 Differences in QAICc values between the different ecological models and the null model for abundance of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age	-50.46	-49.76	-101.25	-113.96	-79.68	-31.66
STP	-75.97	-62.08	-115.01	-118.77	-110.16	-57.15
Gcompo	-96.99	-50.66	-139.02	**-117.04**	-91.84	-66.24
AST	-62.87	-54.02	-69.74	-82.57	-36.51	-78.89

MF: 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 underlined and the QAICc values within 5 units of this model are in bold

The effects of tree stand variables can be summarized into three main results according to our magnitude and “non-negligibility” analyses: (1) negative non-negligible effects: age/type of high even-aged stand, basal area of beech and hornbeam; (2) positive non-negligible effects: standard-with-coppice stands compared to mature high stands; (3) negligible effects: basal area of sessile oak (Tables 3.4 and 3.5). For the effects of skid trail area, it showed non-negligible positive effects on the richness and abundance of PF and NF of successional groups and all light-based groups. The effect of skid trails on the richness and abundance of forest (MF) was negligible (Tables 3.4 and 3.5).

Tree stand effects varied among ecological groups. All the variables that have negative non-negligible effects (age, $STP_{SH\text{-}PH}$, $STP_{PH\text{-}MH}$, G_B, G_H) showed similar trends on richness and abundance data for successional groups: the non-forest group (NF) was the most affected and peri-forest (PF) was second, while forest species (MF) either did not respond or were negatively affected - though less than the other two groups. Such consistent trends were not detected for light-requirement groups, whose response to the different negative effects varied. However, whatever the ecological classification, the effect of mature even-aged forest ($STP_{PH\text{-}MH}$) always influenced ground flora diversity more than the other negative non-negligible effects (age, $STP_{SH\text{-}PH}$, G_B, G_H). Yet, the positive effect of changing stand type from mature even-aged (MH) to standard-with-coppice (SWC) was only found on peri-forest, non-forest species and intermediate-light species (INT), with peri-forest species being the most affected (Tables 3.4 and 3.5).

Multiple-variable models

The results of adding skid trail area as an additional effect to the best tree-stand indicators (STP or Gcompo) are shown in Tables 3.6 and 3.7. Compared to single-variable models (Tables 3.4 and 3.5), the effect of tree stand variables slightly increased or decreased, while the effect of skid trails turned out to be negligible.

Mantel test

A 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 ($r = 0.1788$, $P < 2.22e\text{-}16$).

Influence of sand content

Sand content had a significant effect in the abundance models for four ecological groups. Among them, only the results for two groups (PF and INT) substantially changed: the difference between mature high-forest and SWC decreased and became negligible (Table SM. 3.5 in Supplementary Material).

Species level

Comparing the models for each species with an occurrence >25% (29 species - see Table SM. 3.6 in Supplementary Material) showed that the best models were the ones that related to tree stand properties (age, stand type or total basal area of oak, beech and hornbeam). Our magnitude and negligibility analyses of the combined effects of best tree-stand indicators and skid trail area (Table SM. 3.7 in Supplementary Material) on abundance data revealed a non-negligible negative response of *Isothecium* species and negligible responses of 10 species to the effects of skid trails. However, the influence of skid trails on the remaining species (accounting for 70% of the total species number) was obscure, since statistically it was neither positive/negative nor negligible. Furthermore, when stand type changed from sapling to pole stage ($STP_{SH\text{-}PH}$), the abundance of two species (*Hedera helix and Eunrhynchium striatum*) significantly increased, while the abundance of four species (*Quercus petraea, Ilex aquifolium, Dicranum scoparium, Isothecium sp*) sharply decreased. This was the similar case for $STP_{PH\text{-}MH}$.

Table 3.4 Multiplicative effect of a substantial variation in ecological variables on the richness of the ecological groups (single variable models)

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age(+20 yr)	0.89^{0} [0.87; 0.91]	0.84^{-} [0.80; 0.88]	0.71$^{–}$ [0.67; 0.76]	0.63$^{–}$ [0.57; 0.70]	0.87$^{-,0}$ [0.84; 0.90]	0.83^{-} [0.80; 0.86]
STP_{SH-PH}	0.88$^{-,0}$ [0.86; 0.90]	0.61$^{–}$ [0.60; 0.61]	0.59$^{–}$ [0.58; 0.59]	0.62$^{–}$ [0.61; 0.64]	0.63$^{–}$ [0.62; 0.64]	0.86$^{-,0}$ [0.83; 0.88]
STP_{PH-MH}	0.66$^{–}$ [0.63; 0.68]	0.41$^{–}$ [0.34; 0.47]	0.29$^{–}$ [0.22; 0.37]	0.26$^{–}$ [0.16; 0.38]	0.57$^{–}$ [0.52; 0.62]	0.45$^{–}$ [0.41; 0.50]
STP_{MH-SWC}	1.06^{00} [1.00; 1.14]	1.79^{++} [1.50; 2.21]	1.40^{+} [1.13; 1.81]	0.87 [0.67; 1.26]	1.37^{++} [1.24; 1.53]	1.19 [1.08; 1.34]
G_B(+5 m^2/ha)	0.67$^{–}$ [0.60; 0.75]	0.50$^{–}$ [0.40; 0.62]	0.33$^{–}$ [0.23; 0.45]	0.23$^{–}$ [0.12; 0.39]	0.62$^{–}$ [0.53; 0.71]	0.49$^{–}$ [0.42; 0.58]
G_H(+5 m^2/ha)	0.86^{-} [0.81; 0.91]	0.79^{-} [0.71; 0.88]	0.62$^{–}$ [0.53; 0.72]	0.49$^{–}$ [0.37; 0.63]	0.79^{-} [0.74; 0.85]	0.79^{-} [0.73; 0.86]
G_O(+5 m^2/ha)	0.99^{00} [0.96; 1.02]	0.94^{0} [0.89; 0.99]	0.92^{0} [0.87; 0.98]	0.94^{0} [0.86; 1.03]	0.93^{0} [0.90; 0.96]	0.99^{00} [0.96; 1.04]
AST (+5 %)	1.07^{00} [1.05; 1.1]	1.14^{+} [1.1; 1.18]	1.2^{+} [1.15; 1.25]	1.24^{+} [1.17; 1.32]	1.14^{+} [1.11; 1.17]	1.15^{+} [1.1; 1.19]

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), 5% for skid trails (AST), and a transition from sapling to pole stage in even-aged forests (STP_{SH-PH}), pole to mature stage in even-aged forests (STP_{PH-MH}) and mature even-aged forest to standard-with-coppice stands (STP_{MH-SWC}). “0” and “00” indicate that the effect has a *p*-value of at least 0.95 of being negligible at two different levels. “$^{-}$” and “–” indicate that the effect has a *p*-value of at least 0.95 of being negative and non-negligible at two different levels. “$^{+}$” and “$^{++}$” indicate that the effect has a *p*-value of at least 0.95 of being positive and non-negligible at two different levels (further details are given in the Data analysis section). Values in brackets are 95% confidence intervals of the coefficients.

Table 3.5 Multiplicative effect of a substantial variation in ecological variables on the abundance of the ecological groups (single variable models)

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age(+20 yr)	0.88^{0} [0.85; 0.92]	0.76^{--} [0.70; 0.82]	0.69^{--} [0.62; 0.76]	0.49^{--} [0.42; 0.57]	0.79^{-} [0.75; 0.84]	0.87^{0} [0.82; 0.92]
$STP_{SH\text{-}PH}$	0.60^{--} [0.60; 0.61]	0.74^{--} [0.71; 0.77]	0.50^{--} [0.50; 0.50]	0.54^{--} [0.54; 0.55]	0.82^{-} [0.79; 0.85]	0.47^{--} [0.46; 0.47]
$STP_{PH\text{-}MH}$	0.84^{-} [0.79; 0.90]	0.23^{--} [0.16; 0.32]	0.20^{--} [0.11; 0.31]	0.15^{--} [0.06; 0.28]	0.29^{--} [0.23; 0.35]	0.85 [0.77; 0.92]
$STP_{MH\text{-}SWC}$	0.96 [0.88; 1.06]	1.92^{++} [1.41; 2.84]	2.24^{++} [1.45; 4.08]	0.62 [0.46; 1.05]	1.65^{++} [1.37; 2.05]	1.16 [1.01; 1.35]
G_B(+5 m^2/ha)	0.71^{--} [0.62; 0.81]	0.49^{--} [0.35; 0.67]	0.15^{--} [0.09; 0.23]	0.14^{--} [0.06; 0.29]	0.50^{--} [0.40; 0.62]	0.65 [0.53; 0.79]
G_H(+5 m^2/ha)	0.77^{-} [0.72; 0.83]	0.59^{--} [0.49; 0.71]	0.66^{--} [0.56; 0.77]	0.23^{--} [0.13; 0.36]	0.65^{--} [0.57; 0.73]	0.80^{-} [0.73; 0.88]
G_O(+5 m^2/ha)	0.89^{0} [0.86; 0.92]	0.93^{0} [0.87; 1.00]	0.89^{0} [0.84; 0.95]	0.94^{0} [0.86; 1.04]	0.95^{00} [0.91; 1.00]	$0.86^{-,0}$ [0.82; 0.90]
AST (+5 %)	1.12^{0} [1.09; 1.15]	1.18^{+} [1.12; 1.23]	1.18^{+} [1.12; 1.23]	1.32^{++} [1.22; 1.41]	1.18^{+} [1.12; 1.23]	1.18^{+} [1.14; 1.23]

The legend is the same as for Table 3.4.

Table 3.6 Multiplicative effect of the variables of the best model with skid trails as additional variables on the richness of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)						
STP_{SH-PH}	0.98^{0} [0.85; 1.13]	0.77 [0.62; 0.96]	0.68^{-} [0.53; 0.88]	0.8 [0.55; 1.21]	0.74^{-} [0.63; 0.86]	0.96^{0} [0.8; 1.16]
STP_{PH-MH}	0.66^{--} [0.63; 0.7]	0.42^{--} [0.35; 0.48]	0.3^{--} [0.23; 0.37]	0.27^{--} [0.17; 0.37]	0.58^{--} [0.53; 0.62]	0.46^{--} [0.42; 0.5]
STP_{MH-SWC}	1.07^{0} [1; 1.15]	1.85^{++} [1.55; 2.28]	1.42^{+}[1.14; 1.85]	0.91 [0.7; 1.31]	1.4^{++} [1.26; 1.57]	1.21 [1.09; 1.36]
G_B(+5 m^2/ha)						
G_H(+5 m^2/ha)						
G_O(+5 m^2/ha)						
AST (+5 %)	1.02^{00} [0.99; 1.06]	1.05^{0}[0.99; 1.12]	1.03^{00} [0.96; 1.11]	1.06^{0} [0.95; 1.18]	1.04^{00} [0.99; 1.08]	1.03^{00} [0.98; 1.08]

The legend is the same as for Table 3.4.

Table 3.7 Multiplicative effect of the variables of the best model with skid trails as additional variables on the abundance of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)						
STP$_{SH\text{-}PH}$		1.1 [0.79; 1.57]		0.77 [0.49; 1.24]	1.09 [0.86; 1.38]	
STP$_{PH\text{-}MH}$		0.24^{--} [0.17; 0.32]		0.15^{--} [0.06; 0.28]	0.29^{--} [0.24; 0.35]	
STP$_{MH\text{-}SWC}$		2.03^{++} [1.49; 2.99]		0.65 [0.48; 1.1]	1.71^{++} [1.42; 2.12]	
G_B(+5 m^2/ha)	0.76^{-} [0.65; 0.9]		0.17^{--} [0.1; 0.27]			0.77 [0.62; 0.97]
G_H(+5 m^2/ha)	0.82^{-} [0.75; 0.9]		0.72^{-} [0.59; 0.88]			0.91^{0} [0.8; 1.03]
G_O(+5 m^2/ha)	0.91^{0} [0.87; 0.96]		0.93^{0} [0.85; 1.03]			0.92^{0} [0.86; 0.98]
AST (+5 %)	1.04^{00} [0.99; 1.08]	1.09^{0} [1; 1.19]	1.05^{0} [0.97; 1.13]	1.08^{0} [0.95; 1.23]	1.06^{0} [1; 1.13]	1.08^{0} [1.03; 1.14]

The legend is the same as for Table 3.4.

3.5 Discussion

Though the effects of tree stand attributes and skid trails have been studied previously, no study combined the two factors to detect their effect at stand scale. As a preliminary exploration and an important guide for subsequent research, this study shows that tree stand attributes (expressed as stand type or basal area) are the dominant factors affecting ground flora diversity compared to skid trail area at the 400 m^2 scale. Floristic diversity was higher in standard-with-coppice stands than in mature high-forest stands and decreased with the age of the stand and beech and hornbeam basal area. The effect of sessile oak basal area was negligible. When taking into account tree stand attributes, we found no significant response of light and successional groups to the influence of skid trails at this scale, but we did detect a significant change in species composition when comparing plots with skid trails and without skid trails and there remained a high level of uncertainty regarding the response of individual species.

3.5.1 The best indicators: stand type and basal area

In our study, stand type was the best indicator of ground flora richness (Table 3.2). For abundance, either stand type or basal area of tree species was best, depending on the ecological traits of the ground flora (Table 3.3). For example, stand type best indicated peri-forest species while the basal area of the main tree species best indicated forest and non-forest species abundance. In a similar vein but with a slightly different species mix, Barbier et al., (2009) found that basal area was a better model in French oak-hornbeam lowland forests than models incorporating tree species richness or evenness at the of 400-m^2 plot scale. 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; Nilsson et al., 2008; Sciama et al., 2009; Skov 1997) in managed forest, but few (Barbier, et al., 2009) compared those important variables to detect which one might be the best indicator under the multiple hypotheses framework (Chamberlin, 1965). The effects of skid trails were weak, and the associated models were far from the tree stand attributes models.

3.5.2 The effect of tree stand variables

In the Montargis forest, the majority of current standard-with-coppice stands have not been managed as SWC for decades and are gradually being converted to high forest systems. Generally, the SWC undergo two stages to become a mature high forest: 1) every ten years, low intensity improvement cuts are carried out to maintain 30 mature oaks per hectare; 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). After that, the oak saplings gradually develop into mature high forest. A high-forest rotation is typically 180 to 200 years (Jarret, 2004).

Previous studies have indicated that conversion from SWC to high forest causes high species loss and a decline in ground flora abundance (Baeten et al., 2009; Brewer, 1980; Rooney & Dress, 1997; Van Calster et al., 2007; Van Calster et al., 2008). The SWC forest can provide a wide variety of environmental conditions (e.g. light, temperature, soil acidity) due to regular harvesting or different rotation cycles among stands; this leads to high species diversity in SWC forests (Ash and Barkham, 1976; Packham et al., 1992). In our study, though the SWC stands in the Montargis forest are no longer regularly cut, they still tend to maintain more species than the mature even-aged stands. This higher ground flora diversity is mainly due to the high richness and abundance of the peri-forest and non-forest successional groups or the intermediate-light species group. Though it was not the case in our study, some studies comparing diversity between typical SWC forests (with regular cutting) and high forests found more heliophilous species in SWC stands, such as *Lonicera periclymenum* L., *Rubus fruticosus agg.* and *Ajuga reptans* L. (Baeten et al., 2009; Brown and Oosterhuis, 1981). Other ecological groups which were not included in our research such as vernal species and seed banking species have also been found to prefer the SWC disturbance regime (Ash and Barkham, 1976; Peterken 1981; Rackham 1975).

In our study, the maturing process from young to mature high forest stands is accompanied by a decrease in ground flora diversity, and this decrease is sharper from pole to mature stage than from sapling to pole stage. Our result was consistent with the meta-analysis by Duguid and Ashton (2013). They demonstrated that diversity in managed even-aged old stands (greater than 50 years of age) in temperate forests significantly decreased compared to even-aged young stands or unmanaged stands. Decreases in species richness in mature stands were also found in the studies by Small and McCarthy (2005) and Olivero and Hix (1998). 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 age. For example, Massant et al., (2009) found higher proportions of stress-tolerant species in pure 100-to-150-year-old beech stands and not in other ages classes (5 age classes, intervals of 50 years). The study by Brockerhoff et al. (2003) distinguished adventive and indigenous species and found that the richness and cover of indigenous species was highest in the oldest stands. In our study, the decrease in understory diversity in older forests was mainly due to the loss of many peri-forest and, even more so, of non-forest species. The stand maturing process gradually eliminates early successional groups and facilitates the establishment of mostly forest species.

Yet, 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 – which was the best variable only in a limited number of cases – but we did observe an age effect at species level for the transition from sapling to pole stage or from pole to mature stage. Indeed, at ecological group level, abundance significantly decreased from sapling to pole stage (or from pole to mature stage) for the groups whose best models related to stand type (peri-forest species, shade-tolerant species and intermediate-light species). However, we found a very heterogeneous response to stand age at the species level: the abundance of two species (*H. helix and E. striatum*) significantly and strongly increased while that of four species (*Q. petraea,* *I. aquifolium, D. scoparium, Isothecium sp*) sharply decreased. Furthermore, these heterogeneous responses involved species that belonged to the same ecological group. For example, *Q. petraea, H. Helix and I. aquifolium* belong to the intermediate-light group but two of them had a sharp negative response and one of them had a sharp positive response to stand transition from sapling to pole stage.

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; Brosofske et al., 2001; Nagaike et al., 2005). However, the influence of different tree species in a hardwood forest are dissimilar (Augusto et al., 2003; Brunet et al., 1996; Massant, et al., 2009; Nagaike et al., 2005; Skov, 1997).Our study compared the relative effect of the basal area of oak, beech and hornbeam in an oak-dominant forest. All the successional or light-demanding 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 three studies that compared oak to beech stands (Brunet et al., 1996; Nagaike et al., 2005; Skov, 1997), and a similar negative effect for hornbeam can also be found in Kwiatkowska (1994) and Kwiatkowska et al., (1997), and to some extent in Barbier et al., (2009). As referred to in the studies by Barbier et al., (2009) and Rogers et al., (2008), the decrease in ground flora diversity with increasing basal area of beech or hornbeam could be related to the “mesification” process. Namely, in the successional transition phase, the decline in the dominance of oaks in the overstory is accompanied by an increase in abundance of newly established tree species (beech and hornbeam). As a consequence, the stands might experience a considerable turnover in their understory – more precisely, a decrease in herbaceous species richness and abundance – during this process.

3.5.3 The effect of skid trails

Skid trails have been found to impact soil and vegetation at both small (e.g. on the skid trail, Buckley et al., 2003; Demir et al., 2007; Harvey and Brais, 2002; Lotfalian and Bahmani, 2011) and large spatial scales (e.g. landscapes, Germain and Munsell, 2005; Hosseini et al., 2012). We found three studies on the effects of skid trails at stand scale. In the study by Berger et al., (2004), species richness was proved to be greater on plots (60 m^2) with skid trails than plots off skid trails. Baltzinger et al., (2011) showed that forest paths contributed 42% to the overall plant diversity (400 m^2 plot). Zenner and Berger (2008) found that when plots (60 m^2) exposed to increasing skidder 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 effects of skid trails, the results were consistent with the above studies that skid trails promoted the total ground flora diversity at stand scale; more precsisely, forest species diversity was not affected by skid trails, while peri-forest and non-forest species were significantly favoured. Besides, the diversity of species with different light-demanding levels all increased with increasing skid trail area.

The incorporation of skid trails as additional effects into our best tree-stand indicators did not lead to a significant improvement in the models’ ability to explain variations in ground flora diversity. This indicates that the effects of skid trails on species richness and abundance vanished when other tree stand indices were already incorporated into the statistical model. The explanation for this result might be that our sample plots were selected to cover different stand types, not to represent varied skid trail area among plots. As a result, skid trail area varied significantly among stand types in our study (Table 3.1). Due to this correlation, and to the negligible additional effects of skid trails, we can conclude that, in our case, skid trail effects were negligible for the ecological groups that we studied; the single effects detected were in fact due to differences in skid trail area among stand types. 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 trails from these two traits.

Godefroid and Koedam (2004) showed that the abundance of 61% of the species studied was significantly related to soil compaction. We therefore assumed that individual species would show a significant response to the effects of skid or tractor trails at the stand scale. However, in the results of our investigation at species level, the best models related to tree stand properties (age, stand type or total basal area of oak, beech and hornbeam), with results similar to those at the ecological group level. Furthermore, except for the non-negligible negative response of *Isothecium* species and the negligible responses of some species (Table SM. 7 in Supplementary Material), about 70% of the investigated species (occurrence >25%) showed neither positive/negative nor negligible responses to skid trails. This may be related to a higher level of noise at the species level. Therefore, a higher level of uncertainty for the skid trail effects appeared when we shifted our focus from group level to species level.

3.6 Conclusions

Our results indicate that, in the Montargis forest under current levels of mechanical harvesting, the stand-scale effect of skid trails on the richness and abundance of ecological groups is very likely weak compared to the influence of tree stand attributes. Yet, more uncertainty remains at individual species abundance level, since we did not have a large enough sample to conclude. Considering that mechanical harvesting is becoming more commonly used in forest management, the situation may change; we should expect stronger effects in the long-term, especially if skid trails area increase. Further studies should also include soil density measurements and explore soil types with varying degrees of sensitivity to soil compaction.

3.7 Supplementary Material

Table SM. 3.1 Multiplicative effect of a substantial variation in ecological variables on the richness of the ecological groups (single variable models)

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)	0.89*** [0.87; 0.91]	0.84*** [0.80; 0.88]	0.71*** [0.67; 0.76]	0.63*** [0.57; 0.70]	0.87*** [0.84; 0.90]	0.83***[0.80; 0.86]
STP$_{SH-PH}$	0.88*** [0.86; 0.90]	0.61*** [0.60; 0.61]	0.59*** [0.58; 0.59]	0.62*** [0.61; 0.64]	0.63*** [0.62; 0.64]	0.86*** [0.83; 0.88]
STP$_{PH-MH}$	0.66*** [0.63; 0.68]	0.41*** [0.34; 0.47]	0.29*** [0.22; 0.37]	0.26*** [0.16; 0.38]	0.57*** [0.52; 0.62]	0.45*** [0.41; 0.50]
STP$_{MH-SWC}$	1.06** [1.00; 1.14]	1.79*** [1.50; 2.21]	1.40** [1.13; 1.81]	0.87 [0.67; 1.26]	1.37*** [1.24; 1.53]	1.19** [1.08; 1.34]
G$_B$ (+5 m^2/ha)	0.67*** [0.60; 0.75]	0.50*** [0.40; 0.62]	0.33*** [0.23; 0.45]	0.23*** [0.12; 0.39]	0.62*** [0.53; 0.71]	0.49*** [0.42; 0.58]
G$_H$ (+5 m^2/ha)	0.86*** [0.81; 0.91]	0.79*** [0.71; 0.88]	0.62*** [0.53; 0.72]	0.49*** [0.37; 0.63]	0.79*** [0.74; 0.85]	0.79*** [0.73; 0.86]
G$_O$ (+5 m^2/ha)	0.99 [0.96; 1.02]	0.94* [0.89; 0.99]	0.92** [0.87; 0.98]	0.94 [0.86; 1.03]	0.93*** [0.90; 0.96]	0.99 [0.96; 1.04]
AST (+5 %)	1.07*** [1.05; 1.1]	1.14*** [1.1; 1.18]	1.2*** [1.15; 1.25]	1.24*** [1.17; 1.32]	1.14*** [1.11; 1.17]	1.15*** [1.1; 1.19]

The meanings of the Age, STP, G$_B$, G$_H$, G$_O$, and AST are in table 3.1. MF: forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. 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$_O$), 5% for skid trails (AST), and a transition from sapling to pole stage in even-aged forests (STP$_{SH-PH}$), pole to mature stage in even-aged forests (STP$_{PH-MH}$) and mature even-aged forest to standard-with-coppice stands (STP$_{MH-SWC}$). Levels of statistical significance are symbolized as follows: ****P* < 0.001, ***P* < 0.01, **P* < 0.05.

Table SM. 3.2 Multiplicative effect of a substantial variation in ecological variables on the abundance of the ecological groups (single variable models)

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)	0.88^{***} [0.85; 0.92]	0.76^{***} [0.70; 0.82]	0.69^{***} [0.62; 0.76]	0.49^{***} [0.42; 0.57]	0.79^{***} [0.75; 0.84]	0.87^{***} [0.82; 0.92]
$STP_{SH\text{-}PH}$	0.60^{***} [0.60; 0.61]	0.74^{***} [0.71; 0.77]	0.50^{***} [0.50; 0.50]	0.54^{***} [0.54; 0.55]	0.82^{***} [0.79; 0.85]	0.47^{***} [0.46; 0.47]
$STP_{PH\text{-}MH}$	0.84^{***} [0.79; 0.90]	0.23^{***} [0.16; 0.32]	0.20^{***} [0.11; 0.31]	0.15^{***} [0.06; 0.28]	0.29^{***} [0.23; 0.35]	0.85^{***} [0.77; 0.92]
$STP_{MH\text{-}SWC}$	0.96 [0.88; 1.06]	1.92^{***} [1.41; 2.84]	2.24^{**} [1.45; 4.08]	0.62^{*} [0.46; 1.05]	1.65^{***} [1.37; 2.05]	1.16^{*} [1.01; 1.35]
G_B (+5 m^2/ha)	0.71^{***} [0.62; 0.81]	0.49^{***} [0.35; 0.67]	0.15^{***} [0.09; 0.23]	0.14^{***} [0.06; 0.29]	0.50^{***} [0.40; 0.62]	0.65^{***} [0.53; 0.79]
G_H (+5 m^2/ha)	0.77^{***} [0.72; 0.83]	0.59^{***} [0.49; 0.71]	0.66^{***} [0.56; 0.77]	0.23^{***} [0.13; 0.36]	0.65^{***} [0.57; 0.73]	0.80^{***} [0.73; 0.88]
G_O (+5 m^2/ha)	0.89^{***} [0.86; 0.92]	0.93 [0.87; 1.00]	0.89^{***} [0.84; 0.95]	0.94 [0.86; 1.04]	0.95 [0.91; 1.00]	0.86^{***} [0.82; 0.90]
AST (+ 5%)	1.12^{***} [1.09; 1.15]	1.18^{***} [1.12; 1.23]	1.18^{***} [1.12; 1.23]	1.32^{***} [1.22; 1.41]	1.18^{***} [1.12; 1.23]	1.18^{***} [1.14; 1.23]

The meanings of the Age, STP, G_B, G_H, G_O and AST are in table 3.1. MF: forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. 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), 5% for skid trails (AST), 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 standard-with-coppice stands ($STP_{MH\text{-}SWC}$). Levels of statistical significance are symbolized as follows: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

Table SM. 3.3 Multiplicative effect of the variables of the best model with skid trails as additional variables on the richness of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)						
$STP_{SH\text{-}PH}$	0.98 [0.85; 1.13]	0.77^{*} [0.62; 0.96]	0.68^{**} [0.53; 0.88]	0.8 [0.55; 1.21]	0.74^{***} [0.63; 0.86]	0.96 [0.8; 1.16]
$STP_{PH\text{-}MH}$	0.66^{***} [0.63; 0.7]	0.42^{***} [0.35; 0.48]	0.3^{***} [0.23; 0.37]	0.27^{***} [0.17; 0.37]	0.58^{***} [0.53; 0.62]	0.46^{***} [0.42; 0.5]
$STP_{MH\text{-}SWC}$	1.07^{*} [1; 1.15]	1.85^{***} [1.55; 2.28]	1.42^{**} [1.14; 1.85]	0.91 [0.7; 1.31]	1.4^{***} [1.26; 1.57]	1.21^{***} [1.09; 1.36]
G_B (+5 m^2/ha)						
G_H (+5 m^2/ha)						
G_O (+5 m^2/ha)						
AST (+ 5%)	1.02 [0.99; 1.06]	1.05 [0.99; 1.12]	1.03 [0.96; 1.11]	1.06 [0.95; 1.18]	1.04 [0.99; 1.08]	1.03 [0.98; 1.08]

The meanings of the Age, STP, G_B, G_H, G_O, and AST are in table 3.1. MF: forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. 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), 5% for skid trails (AST), 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 standard-with-coppice stands ($STP_{MH\text{-}SWC}$). Levels of statistical significance are symbolized as follows: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

Table SM. 3.4 Multiplicative effect of the variables of the best model with skid trails as additional variables on the abundance of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)						
$STP_{SH\text{-}PH}$		1.1 [0.79; 1.57]		0.77 [0.49; 1.24]	1.09 [0.86; 1.38]	
$STP_{PH\text{-}MH}$		0.24^{***} [0.17; 0.32]		0.15^{***} [0.06; 0.28]	0.29^{***} [0.24; 0.35]	
$STP_{MH\text{-}SWC}$		2.03 [1.49; 2.99]		0.65^{*} [0.48; 1.1]	1.71^{***} [1.42; 2.12]	
G_B (+5 m^2/ha)	0.76^{**} [0.65; 0.9]		0.17^{***} [0.1; 0.27]			0.77^{*} [0.62; 0.97]
G_H (+5 m^2/ha)	0.82^{***} [0.75; 0.9]		0.72^{**} [0.59; 0.88]			0.91 [0.8; 1.03]
G_O (+5 m^2/ha)	0.91^{***} [0.87; 0.96]		0.93 [0.85; 1.03]			0.92^{**} [0.86; 0.98]
AST (+ 5%)	1.04 [0.99; 1.08]	1.09^{*} [1; 1.19]	1.05 [0.97; 1.13]	1.08 [0.95; 1.23]	1.06^{*} [1; 1.13]	1.08^{**} [1.03; 1.14]

The meanings of the Age, STP, G_B, G_H, G_O and AST are in table 3.1. MF: forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. 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), 5% for skid trails (AST), 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 standard-with-coppice stands ($STP_{MH\text{-}SWC}$). Levels of statistical significance are symbolized as follows: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Table SM. 3.5 Multiplicative effect of the variables of the best model with sand content as an additional variable on the abundance of the ecological groups

	Successional status			Light preference		
	MF	PF	NF	SHA	INT	HEL
Age (+20 yr)						
$STP_{SH\text{-}PH}$		0.82^{00} [0.78; 0.85]		$0.48^{–}$ [0.41; 0.55]	0.88^{00} [0.85; 0.90]	
$STP_{PH\text{-}MH}$		$0.30^{–}$ [0.22; 0.39]		$0.12^{–}$ [0.06; 0.20]	$0.33^{–}$ [0.28; 0.39]	
$STP_{MH\text{-}SWC}$		1.33^{00} [0.94; 1.92]		0.85 [0.51; 1.40]	1.33^{0} [1.08; 1.65]	
G_B (+5 m^2/ha)	0.69 [0.60; 0.78]		$0.16^{–}$ [0.10; 0.24]			0.64^{-} [0.52; 0.77]
G_H (+5 m^2/ha)	0.77^{0} [0.72; 0.83]		0.65^{-} [0.56; 0.75]			0.80^{0} [0.73; 0.88]
G_O (+5 m^2/ha)	0.88^{00} [0.85; 0.91]		0.91^{00} [0.86; 0.97]			0.85^{00} [0.81; 0.90]
Sand (+10%)	1.09^{00} [1.04; 1.15]	0.82^{0} [0.72; 0.92]	0.81^{0} [0.71; 0.91]	1.23^{0} [0.95; 1.58]	0.89^{00} [0.82; 0.96]	1.04^{00} [0.96; 1.12]

The meanings of the Age, STP, G_B, G_H and G_O are in table 3.1. MF: forest species, PF: peri-forest species, NF: non-forest species, SHA: shade-tolerant species, INT: intermediate-light species, HEL: heliophilous species. 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 sand content (Sand), and a transition from sapling to pole stage in even-aged forest ($STP_{SH\text{-}PH}$), pole to mature stage in even-aged forest ($STP_{PH\text{-}MH}$) and mature even-aged forest to standard-with-coppice stands ($STP_{MH\text{-}SWC}$). “0” and “00” indicate that the effect has a *p*-value of at least 0.95 of being negligible at two different levels. “$^{-}$” and “–” indicate that the effect has a *p*-value of at least 0.95 of being negative and non-negligible at two different levels. “$^{+}$” and “$^{++}$” indicate that the effect has a *p*-value of at least 0.95 of being positive and non-negligible at two different levels (further details are given in the section of Data analysis). Values in brackets are 95% confidence intervals of the coefficients.

Table SM. 3.6 Differences in QAICc values between the different ecological models and the null model for species abundance

Species	Age	STP	Gcompo	AST
Carpinus betulus	-7.08	-5.11	-18.29	-5.90
Fagus sylvatica	-21.99	-26.10	-34.24	-17.31
Quercus petraea	-13.22	-67.68	-39.19	-61.42
Sorbus torminalis	0.45	3.82	0.46	1.39
Hedera helix	2.05	-20.73	-5.11	-1.58
Ilex aquifolium	1.92	-4.23	4.10	0.48
Lonicera periclymenum	-7.65	-22.43	-12.62	1.84
Rubus fruticosus	-15.08	-32.68	-15.65	-3.10
Carex pilulifera	1.77	1.42	-8.13	-0.04
Deschampsia flexuosa	-24.58	-31.32	-46.69	-36.07
Festuca heterophylla	-27.03	-23.13	-28.54	-6.93
Holcus mollis	-4.00	-18.29	-19.88	-11.08
Luzula forsteri & multiflora	-48.41	-58.53	-59.09	-7.97
Poa nemoralis	-56.58	-60.01	-60.14	-28.16
Teucrium scorodonia	-44.53	-49.17	-40.12	-19.23
Viola riviniana & reichenbachiana	-35.96	-26.39	-19.00	-10.29
Atrichum undulatum	-8.01	-1.77	-6.10	0.73
Brachythecium rutabulum	1.72	2.67	3.22	1.17
Dicranella heteromalla	-0.04	-0.48	0.44	-1.26
Dicranum scoparium	-5.63	-5.72	1.20	1.91
Eunrhynchium stokesii & praelongum	1.98	-7.24	-2.34	0.42
Eunrhynchium striatum	0.58	-5.20	1.30	-0.73
Fissidens sp	1.69	1.72	5.33	0.68
Hypnum cupressiforme	-32.82	-44.31	-13.30	-20.51
Isothecium sp	-2.23	2.68	1.25	-0.02
Lophocolea sp	1.02	4.23	-3.10	1.69
Polytricum formosum	-2.76	-20.26	-9.64	-6.89
Scleropodium purum	-4.16	-3.88	-6.28	-6.33
Thuidium tamariscinum	-7.08	-5.11	-18.29	-5.90

The meanings of the Age, STP, Gcompo and AST are in table 3.1. The smaller the QAICc, the better the model with respect to the others. The model with the smallest QAICc is underlined for each species. Some species aggregates were defined (*Luzula forsteri & multiflora, Viola riviniana & reichenbachiana, Eunrhynchium stokesii& praelongum*) due to identification problems. Some taxa were determined only at the genus level due to lack of information to identify the species (*Fissidens sp, Isothecium sp, Lophocolea sp*).

Table SM. 3.7 Multiplicative effect of the variables of the best model with skid trails as an additional variable on the species abundance

Species	Age (+20 yr)	STP$_{SH-PH}$	STP$_{PH-MH}$	STP$_{MH-SWC}$	GB (+5 m^2/ha)	GH (+5 m^2/ha)	GQ (+5 m^2/ha)	AST (+5 %)
Atrichum undulatum	$0.63^{--,***}$ [0.54; 0.74]							0.95^{0} [0.86; 1.05]
Brachythecium rutabulum	$0.6^{--,**}$ [0.42; 0.83]							0.87 [0.67; 1.08]
Lophocolea sp	1.23 [0.93; 1.66]							0.98 [0.7; 1.28]
Quercus petraea		$0.32^{--,***}$ [0.27; 0.38]	$2.42^{++,***}$ [2.36; 2.5]	0.87^{*} [0.77; 1.01]				1.16^{***} [1.07; 1.25]
Hedera helix		$7.42^{++,***}$ [2.81; 22.22]	$0.27^{--,***}$ [0.17; 0.38]	$2.69^{++,***}$ [1.74; 4.84]				1.09 [0.9; 1.31]
Ilex aquifolium		$0.12^{--,***}$ [0.07; 0.16]	0.23 [0; 0.83]	15.85 [2.14;98197.43]				0.97 [0.69; 1.34]
Lonicera periclymenum		1.35 [0.82; 2.3]	$0.34^{--,***}$ [0.26; 0.42]	1.29 [1.01; 1.77]				0.95^{0} [0.83; 1.07]
Rubus fruticosus		1.86 [1.02; 3.58]	$0.13^{--,***}$ [0.06; 0.23]	$2.99^{++,**}$ [1.7; 6.98]				1.06^{0} [0.91; 1.22]
Viola riviniana & reichenbachiana		1.86 [1.02; 3.58]	$0.13^{--,***}$ [0.06; 0.23]	$2.99^{++,**}$ [1.7; 6.98]				1.06^{0} [0.91; 1.22]
Dicranum scoparium		$0.15^{--,***}$ [0.07; 0.28]	0.54 [0.05; 1.01]	2.29 [0.79; 51.6]				0.93 [0.63; 1.34]
Eunrhynchium stokesii & praelongum		0.49 [0.18; 1.54]	$0.54^{--,***}$ [0.34; 0.71]	$0.32^{--,***}$ [0.28; 0.39]				0.77 [0.54; 1.04]
Eunrhynchium striatum		$2.91^{++,**}$ [1.39; 6.54]	$0.46^{--,***}$ [0.35; 0.56]	$1.64^{++,**}$ [1.21; 2.4]				1.04^{0} [0.88; 1.22]
Fissidens sp		0.74 [0.13; 9.7]	0.04^{--} [0; 0.18]	4.96 [1.12; 728.95]				$0.5^{-,*}$ [0.26; 0.86]
Hypnum cupressiforme		1.57 [0.4; 22.08]	$12.54^{++,***}$ [7.92; 23.93]	$0.5^{--,***}$ [0.44; 0.57]				0.82 [0.6; 1.08]
Isothecium sp		$0.01^{--,***}$ [0; 0.02]	$2.41^{++,**}$ [2.02; 6.56]	6.08 [1.51; 351.55]				0.88 [0.7; 1.11]

Carpinus betulus	$0.4^{--,***}$ [0.24; 0.64]	0.92 [0.73; 1.15]	0.91 [0.8; 1.03]	0.99^{0} [0.89; 1.1]
Fagus sylvatica	$2.51^{++,***}$ [1.5; 4.18]	0.9 [0.61; 1.3]	0.9 [0.71; 1.14]	0.76^{*} [0.59; 0.95]
Carex pilulifera	0.88 [0.47; 1.59]	$0.45^{--,**}$ [0.27; 0.72]	0.84 [0.68; 1.04]	0.91 [0.75; 1.09]
Deschampsia flexuosa	$0.45^{--,**}$ [0.26; 0.75]	$0.62^{--,**}$ [0.45; 0.83]	0.95^{0} [0.84; 1.09]	1.08^{0} [0.96; 1.2]
Festuca heterophylla	$0.54^{--,**}$ [0.37; 0.78]	0.75^{*} [0.6; 0.94]	1.06^{0} [0.95; 1.18]	1.02^{00} [0.93; 1.11]
Holcus mollis	$0.47^{--,*}$ [0.25; 0.87]	$0.65^{-,*}$ [0.46; 0.9]	$0.74^{-,***}$ [0.62; 0.88]	0.93 [0.79; 1.08]
Luzula forsteri & multiflora	$0.01^{--,**}$ [0; 0.13]	0.79 [0.47; 1.23]	0.91 [0.75; 1.1]	1.17^{*} [1; 1.36]
Poa nemoralis	$0^{--,***}$ [0; 0.05]	$0.39^{--,**}$ [0.19; 0.74]	1.06 [0.84; 1.34]	0.94 [0.76; 1.14]
Teucrium scorodonia	$0.21^{--,***}$ [0.08; 0.48]	$0.35^{--,***}$ [0.19; 0.59]	1.02^{0} [0.86; 1.21]	1.05^{0} [0.91; 1.21]
Polytricum formosum	0.95 [0.66; 1.37]	1.18 [0.97; 1.43]	0.95^{0} [0.84; 1.07]	1.03^{0} [0.93; 1.14]
Thuidium tamariscinum	0.87 [0.5; 1.5]	1.14 [0.84; 1.53]	0.88 [0.72; 1.08]	0.83 [0.68; 1]

The meanings of the Age, STP, G_B, G_H, G_O and AST are in table 3.1. 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), 5% for skid trails (AST), and a transition from sapling to pole stage in even-aged forests (STP_{SH-PH}), pole to mature stage in even-aged forests (STP_{PH-MH}) and mature even-aged forest to standard-with-coppice stands (STP_{MH-SWC}). “0” and “00” indicate that the effect has a p-value of at least 0.95 of being negligible at two different levels. “$^{-}$” and “–” indicate that the effect has a *p*-value of at least 0.95 of being negative and non-negligible at two different levels. “$^{+}$” and “$^{++}$” indicate that the effect has a *p*-value of at least 0.95 of being positive and non-negligible at two different levels (further details are given in the Data analysis section). Values in brackets are 95% confidence intervals of the coefficients. Levels of statistical significance are symbolized as follows: $***P < 0.001$, $**P < 0.01$, $*P < 0.05$.

Table SM. 3.8 Species list and ecological trait

Species	**Successional status**	**Light**
Acer campestre L.	forest	heliophilous
Betula pendula Roth	forest	heliophilous
Carpinus betulus L.	forest	
Fagus sylvatica L.	forest	
Picea abies (L.) Karsten	forest	heliophilous
Pinus sylvestris L.	forest	heliophilous
Populus tremula L.	forest	heliophilous
Prunus avium L.	forest	heliophilous
Quercus robur L. subsp. robur	forest	heliophilous
Quercus petraea Liebl. subsp. petraea	forest	heliophilous
Robinia pseudoacacia L.	forest	heliophilous
Sorbus domestica L.	forest	heliophilous
Sorbus torminalis (L.) Crantz	forest	heliophilous
Calluna vulgaris (L.) Hull	non-forest	heliophilous
Cornus sanguinea L. subsp. sanguinea	peri-forest	heliophilous
Corylus avellana L.	peri-forest	heliophilous
Crataegus laevigata (Poiret) DC.	peri-forest	heliophilous
Crataegus monogyna Jacq.	peri-forest	heliophilous
Cytisus scoparius (L.) Link	peri-forest	intermediate
Erica cinerea L.	non-forest	heliophilous
Hedera helix L.	forest	intermediate
Ilex aquifolium L.	peri-forest	shade
Lonicera periclymenum L.	forest	intermediate
Malus sylvestris Miller	peri-forest	intermediate
Prunus padus L. subsp. padus	peri-forest	intermediate
Prunus spinosa L.	peri-forest	heliophilous

Rosa arvensis Hudson	peri-forest	
Rosa canina L. subsp. *canina* var. *lutetiana* (Léman ex Cass.) Baker	peri-forest	
Rubus fruticosus L.	peri-forest	intermediate
Ruscus aculeatus L.	forest	
Salix caprea L.	peri-forest	intermediate
Salix cinerea L.	peri-forest	heliophilous
Solanum dulcamara L.	non-forest	heliophilous
Agrostis capillaris L.	non-forest	heliophilous
Ajuga reptans L.	non-forest	heliophilous
Anemone nemorosa L.	forest	heliophilous
Anthoxanthum odoratum L. subsp. *nipponicum* (Honda) Tzvelev	non-forest	heliophilous
Arum maculatum L.	forest	shade
Brachypodium sylvaticum (Hudson) P. Beauv.	peri-forest	intermediate
Bromus hordeaceus L. subsp. *hordeaceus* écoph. vivace	non-forest	heliophilous
Calamagrostis epigejos (L.) Roth	peri-forest	heliophilous
Campanula rapunculus L.	non-forest	
Carex flacca Schreber	non-forest	
Carex spicata Huds.	non-forest	intermediate
Carex ovalis Good.	non-forest	heliophilous
Carex pallescens L.	non-forest	
Carex pilulifera L.	non-forest	intermediate
Carex sylvatica Hudson	forest	shade
Centaurium erythraea Rafn	non-forest	shade
Cirsium palustre (L.) Scop.	non-forest	heliophilous
Dactylis glomerata L.	non-forest	heliophilous
Deschampsia cespitosa (L.) P. Beauv.	non-forest	intermediate

Deschampsia flexuosa (L.) Trin.	non-forest	heliophilous
Dianthus armeria L. subsp. *armeria*	non-forest	
Digitalis purpurea L. var. *purpurea*	peri-forest	intermediate
Epilobium angustifolium L. subsp. *angustifolium*	peri-forest	heliophilous
Epilobium tetragonum L.	non-forest	heliophilous
Eupatorium cannabinum L.	non-forest	intermediate
Euphorbia amygdaloides L.	forest	intermediate
Euphorbia dulcis L. subsp. *incompta* (Ces.) Nyman	forest	intermediate
Festuca heterophylla Lam.	forest	shade
Festuca filiformis Pourr.	non-forest	heliophilous
Fragaria vesca L.	non-forest	heliophilous
Galeopsis tetrahit L.	peri-forest	heliophilous
Galium aparine L.	peri-forest	intermediate
Galium mollugo L.	non-forest	heliophilous
Galium odoratum (L.) Scop.	forest	shade
Galium palustre L.	non-forest	intermediate
Geranium dissectum L.	peri-forest	heliophilous
Geranium robertianum L.	peri-forest	intermediate
Hieracium vulgatum Fr.	non-forest	heliophilous
Holcus lanatus L.	non-forest	heliophilous
Holcus mollis L.	non-forest	intermediate
Hyacinthoides non-scripta (L.) Chouard ex Rothm.	forest	intermediate
Hypericum perforatum L.	peri-forest	heliophilous
Hypericum pulchrum L.	non-forest	heliophilous
Lamium galeobdolon L.	forest	shade
Lapsana communis L.	peri-forest	intermediate

Lathyrus linifolius subsp. *montanus* (Bernh.) Bässler	non-forest	intermediate
Linum catharticum L. var. *catharticum*	non-forest	heliophilous
Luzula pilosa (L.) Willd.	forest	shade
Melampyrum pratense L.	non-forest	intermediate
Melica uniflora Retz.	forest	shade
Melittis melissophyllum L.	non-forest	intermediate
Milium effusum L.	forest	shade
Moehringia trinervia (L.) Clairv.	peri-forest	intermediate
Monotropa hypopithys L.	forest	shade
Myosotis arvensis Hill	peri-forest	
Phleum pratense L. subsp. *pratense*	non-forest	heliophilous
Phytolacca americana L.	peri-forest	intermediate
Plantago lanceolata L.	non-forest	heliophilous
Poa chaixii Vill. in Gilib.	non-forest	heliophilous
Poa nemoralis L.	forest	shade
Poa trivialis L.	non-forest	heliophilous
Polygala vulgaris L. var. *transiens*	non-forest	heliophilous
Polygonatum multiflorum (L.) All.	forest	intermediate
Potentilla sterilis (L.) Garcke	non-forest	intermediate
Primula veris L. subsp. *veris*	non-forest	heliophilous
Prunella vulgaris L.	non-forest	heliophilous
Ranunculus acris L. subsp. *acris*	non-forest	intermediate
Rumex acetosella L. subsp. *acetosella* var. *acetosella*	non-forest	heliophilous
Sagina apetala Ard. subsp. *apetala*	peri-forest	heliophilous
Scrophularia nodosa L.	peri-forest	intermediate
Senecio jacobaea L. subsp. *jacobaea*	peri-forest	heliophilous
Senecio sylvaticus L.	peri-forest	intermediate

Solidago virgaurea L.	non-forest	intermediate
Sonchus asper (L.) Hill	peri-forest	heliophilous
Stachys officinalis (L.) Trévisan	non-forest	intermediate
Stachys sylvatica L.	peri-forest	shade
Stellaria holostea L.	non-forest	intermediate
Succisa pratensis Moench	non-forest	heliophilous
Teucrium scorodonia L.	non-forest	intermediate
Valeriana officinalis subsp. *repens* 4, 6	non-forest	heliophilous
Veronica chamaedrys L.	non-forest	intermediate
Veronica montana L.	non-forest	shade
Veronica officinalis L.	non-forest	
Vicia sativa L. subsp. sativa	peri-forest	heliophilous
Vicia tetrasperma (L.) Schreber	peri-forest	heliophilous
Vinca minor L.	forest	intermediate
Dryopteris affinis (Lowe) Fraser-Jenkins	forest	shade
Dryopteris carthusiana (Vill.) H.P. Fuchs	forest	shade
Dryopteris filix-mas (L.) Schott	forest	shade
Pteridium aquilinum (L.) Kuhn	peri-forest	heliophilous

Data source: Julve, 2007. The blanks in the table mean information is lacking and the species is not classified. For successional status, we classified the species into three groups following Julve (2002) as in Barbier et al., (2009): (i) forest species whose preferred habitat is mature forests, (ii) peri-forest species whose habitats are found close to mature forests either temporally (in the early stages of succession) or spatially (along edges), and (iii) non-forest species whose preferred habitats are not linked to forests. We also distinguished three groups according to light preference (Ellenberg indicator value L, Ellenberg et al., 1992): shade-tolerant ($L < 5$); intermediate light ($5 \leq L < 7$), and heliophilous ($L \geq 7$) .

Chapter IV Plant diversity patterns on skid trails in high forest oak stands of different ages and links to soil moisture, soil compaction and light

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4.1 Abstract

Increasingly mechanized timber harvesting and repeated use of permanent skid trail networks may affect the growth and diversity of ground vegetation differently at subsequent stages in the rotation. At fine scale, no studies compared the influence of micro-environmental factors and the effects of skid trail disturbance on ground flora diversity. We investigated understory diversity patterns on and off skid trails in 12 x 3 (36) oak even-aged stands 30, 50 and 63 years old in the northern half of France. Sampling subplots were placed in four locations: skid trail centre, wheel track, skid trail edge plus an off-trail control plot inside the forest. At each 5-by-0.5m subplot, we measured soil moisture, soil compaction (penetration resistance and bulk density) and PAR (photosynthetic active radiation) and recorded the abundance of all the vascular plants. We analyzed plant response to subplot location, micro-enviromental factors (soil moisture, soil compaction, light) and stand attribute (stand type, basal area) at the individual species and at ecological group levels. The species were assigned to ecological groups according to life form, seed bank persistence, light preference and moisture requirements. For each species and ecological group, we selected the best of 27 *a priori* relevant, generalized linear mixed models (GLMMs) and assessed the magnitude of the effects of each variable. 1) Soil compaction, soil moisture and light significantly varied among stand types. Higher soil compaction was detected on the tracks of skid trails in the 50 and 63 years old stands, while soil moisture and light did not vary with subplot location whatever the stand type. 2) At species group level, the best models included subplot location, soil moisture or soil compaction. Compared to the control plots, skid trails had higher richness of tree and short-term seed bank species in the 50- and 63-year-old stands. The abundance of tree and shade-tolerant species was also higher on skid trails. Soil moisture was strongly positively correlated with the richness of low- and high- humidity species, shade-tolerant species and transient seed bank species as well as with the abundance of short-term seed bank species. Bulk density positively affected heliophilous species richness, while penetration resistance was related to shrub abundance; 3) At species level, subplot location was the only factor that showed non-negligible effects on species abundance. Higher species abundance on skid trails occurred in the 30- and 63-year-old stands.Subplot location, soil moisture and soil compaction played dominant roles at fine scale in stands managed with skid trail system. Skid trails in our research area promote ground flora diversity, with no detected

negative effect. Longer-term study of skid trail effects would be needed to validate the main findings of our study.

4.2 Introduction

During the last decades, manual felling and logging for forest management has evolved towards mechanized harvesting. Mechanized logging and timber harvesting rely on permanent evenly-distributed skid trail systems (Lorente et al., 2012), which has the advantage of confining the disturbances to relatively smaller areas (Akbarimehr and Jalilvand 2013) while providing easy access to forest interior (Avon et al., 2013). Micro-site environment on skid trails might differ from interior forest, such as canopy opening, higher soil compaction, soil nutrient loss or increased soil moisture on skid trails compared to undisturbed habitat (Buckley et al., 2003; Hattori et al., 2003; Zenner and Berger, 2008). These environmental changes might explain the differences of ground flora observed between the locations on and off skid trails (Brais, 2002; Swaine and Agyeman, 2008; Wolf, 2008; Harvey and Avon et al., 2013).

Canopy cover is one of the most important factors that control a site’s microclimate (Metzger and Schultz, 1984). Opening canopy on skid trails can influence plant growth and competition patterns, especially between shade tolerant and intolerant species (Horn, 1971; Planchais and Sinoquet, 1998). However, light level may not always stay high on skid trails years after logging or cutting operations. The duration of canopy closure together with residual tree stands properties (age, height...) can largely regulate light availability on skid trails.

Soil compaction, a reduction in the volume of a given mass of soil (Glinski and Lipiec, 1990), is one of the major consequences of mechanized harvesting on skid trails (Najafi et al., 2009; Ampoorter et al, 2010; Naghdi et al., 2010; Solgi and Najafi, 2014). Therefore it is often used as an indicator of forest floor disturbance resulting from the machine use on skid trails. Not only is the soil under the tyres impacted, but also the soil around it (Ampoorter et al., 2010). Compaction changes soil structure (Akbarimehr and Naghdi, 2012), reduces porosity (Gent et al., 1984), increases bulk density (Akay et al., 2007; Lotfalian and Bahmani, 2011) and water runoff (Najafi et al., 2009) thereby inducing soil erosion (Jusoff, 1996). Very few studies so far directly related ground flora to soil compaction measured from skid trails, so that the role of compaction from skid trails is still a hypothesis to be validated. For instance, Buckley et al., (2003) measured soil compaction degree as a description of the growth conditions on skid trails, but did not directly link it to ground flora diversity in the statistical analyses. Some studies investigated the effects of soil compaction (penetration resistance or bulk density) in the area covered by skid trails on ground flora, however, their investigation were at stand scale (100 m^2 or 60 m^2 plots) (Hattori et al., 2013; Zenner and Berger, 2008; Berger et al ., 2004). In fact, we found only two studies investigating the relationship between soil compaction on skid trails and ground flora. Yet, their results were not consistent. Roovers et al., (2004) demonstrated that the intensity of soil compaction was highly correlated with species cover (negatively) and composition. On the contrary, Heninger et al., (2002) found that reduced Douglas-fir tree seedling height on skid trails was unrelated to percentage increases in soil bulk density. Since the recovery process of soil compaction may take several decades or even centuries (Greacen and Sands, 1980; Croke et al., 2001; Godefroid and Koedam, 2004), and could vary a lot at local scale, we assumed that it might also be an important soil property affecting the regeneration and growth of ground flora.

Soil moisture is an important fine-scale factor affecting plant in many studies (Beckage et al., 2000; Beckage et al., 2008; Gray et al., 2012) but those dealing with skid trails did not find consistent results. For example, some studies demonstrated that soil moisture was higher on skid trails due to the removal of canopy cover that reduced rainfall intercept and increased water intercept in the soil, while some found decreased water holding ability on wheel rut after the first machine passes (Miller and Sirois, 1986; Buckely, et al., 2003; Solgi and Najafi, 2004; Ezzati et al., 2012). Since the influence of canopy cover and machine use on soil moisture have not been jointly compared in a study, we still need to study the soil moisture level on skid trials and its relation to canopy cover and soil disturbance.

The relative importance of different environmental or history filters (e.g. disturbance) for ground flora diversity may vary with forest stage or development (Burton et al., 2011). Stands of different ages and types within a forest most frequently experience different management regimes, i.e. they are subjected to varying intensities of machinery use and different distribution patterns of skid trails (Zenner 2007; Zenner and Berger, 2008). Besides, more mature forests managed with large sized machines need wider skid trails for wood extraction, potentially leading to the creation of deeper continuous ruts (Schack-Kirchner et al., 2007; Rodolfo Picchio 2012). Futhermore, trees at different ages may intercept different levels of light and water. Limited researches compared the diversity pattern on skid trails in different forest types. Roovers et al., (2004) examined the effects of trampling skid trails on vegetation along trails in four vegetation types: two deciduous forest types, one grassland and one heathland, and showed that the increase in floristic dissimilarity from trail to undisturbed vegetation was higher in forests than in grassland and heathland, whereas no difference was detected between the two forests types. Liechty et al., (2002) and Beaudet (2014) proved that regeneration failures occurred on skid trails in stands harvested using single-tree selection but not in stands with shelterwoods or clearcuts. Besides, Swaine (2008) investigated timber tree regeneration on skid trails in two forest reserves in first and second rotations respectively. However, these studies were not enough informative for drawing conclusions on the exact role skid trails played in different forests.

Fine-scale studies of diversity pattern can provide insights into how historical and environmental filters interact across scales to influence vegetation locally (Leibold et al., 2004; Burton et al., 2011). No previous studies have ever compared the influence of micro-environmental factors with skid trail disturbance to detect their effects on ground flora diversity. Our study intended to investigate fine-scale understory diversity pattern in three high forest types of varying tree maturity with skid trail system, as well as to find out the dominant factors affecting ground flora diversity among subplot location, soil moisture, soil compaction, light, stand type and basal area. For subplot location, we used subplots on and off skid trails to indirectly represent habitat exposed to frequent and infrequent disturbances. In addition, within skid trails, we used different types of location - middle of skid trails, wheel track and edge of skid trails - to represent the disturbance gradient within skid trails. The research objectives were: 1) What is the relative importance of subplot location, soil moisture, soil compaction and light on ground flora diversity? 2) Does it depend on stand types? 3) Are the dominant factors different among ecological groups?

4.3 Material and methods

4.3.1 Study area

The Montargis forest (4,090 ha, 48°01' N, 2°48' E, Loiret, northern half of France) is an ancient state forest managed by the French National Forestry Office (ONF) around 110 km south of Paris. Elevation ranges from 95 to 132 m a.s.l. Climate is oceanic with a mean annual rainfall and temperature of about 647 mm and 10.9 °C respectively (Chevalier, 2003). The soil conditions are homogeneous, with plateau soils on chalk substrate. There are small variations in soil texture (sandy to silt-sandy) and stone content (Chevalier, 2003). Dominant tree species are sessile oak (*Quercus petraea*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). The main management goal is to produce quality timber. Therefore, 70% of the area is managed as an oak even-aged high forest. Former standard-with-coppice (SWC) forest management with sessile oak as standards and hornbeam as coppice has been progressively replaced since 1857 by an even-aged high forest system dominated by oak. A high-forest cycle rotation is typically 180 to 200 years until trees reach 80 cm in diameter (ONF, 1996; Jarret, 2004). All even-aged high-forest stands have experienced the typical seed-tree natural regeneration phase.

4.3.2 Data collection

We set 20m-×-20m quadrats in 36 even-aged high stands representing three stand types of different average ages (30, 50 and 63-years old, 12 quadrats per stand type; respectively STP30, STP50 and STP63). To extract wood out of the stand without disturbing the whole soil surface, parallel skid trails are set up approximately every 22 m. The width and rut depth of skid trails increase with stand age (Fig.4.1). We set up a 22m-radius circular plot from the center of the quadrats for dendrometry, measuring diameter at breast height (“DBH”, in cm) for each tree as Chevalier (2003) did.

We made vegetation investigation and measured penetration resistance (PR), bulk density (BD) and light on four 0.5m-×-5m subplots systematically set in each 400m^2 quadrat (Fig. 4.2 (a)): (1) on the wheel track of skid trail (TR); (2) between the two wheel tracks of skid trail (BE); (3) on the edge of the skid trail (BO); (4) on the midpoint between two skid trails as control (CO). These four subplots have the same direction as the skid trail, and their centers are aligned orthogonally to the skid trail. The investigated skid trail was the one that covered the largest area within the selected quadrats (Fig. 4.2 (a)).

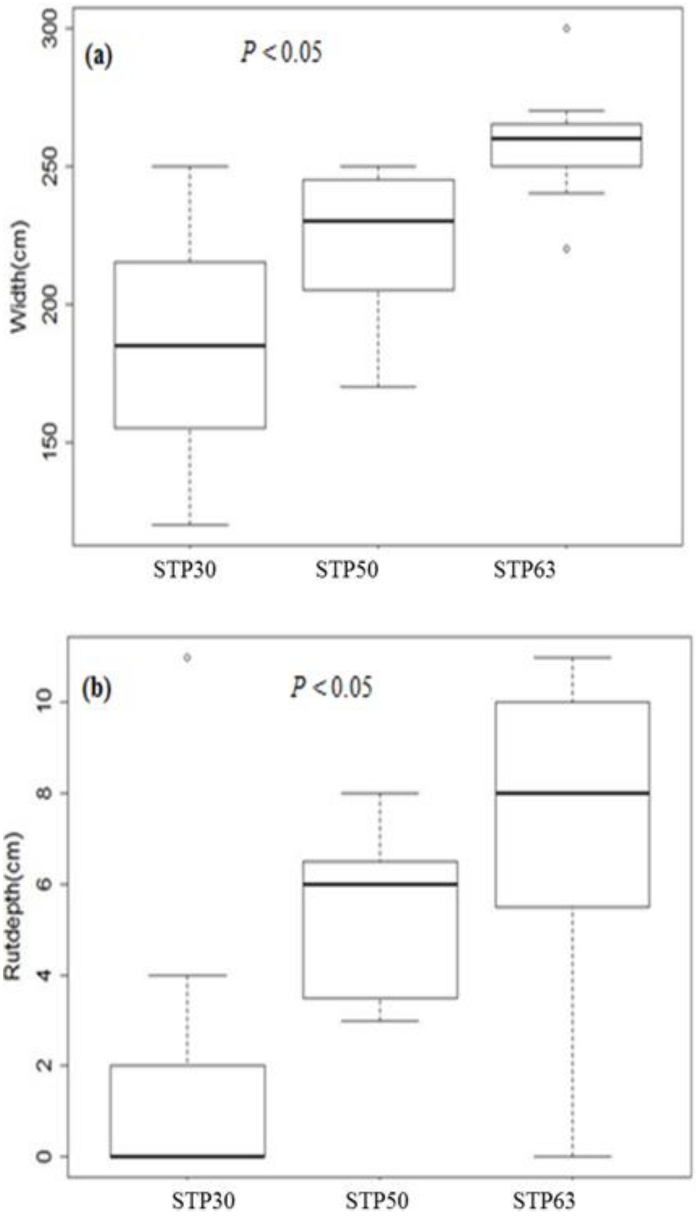


Figure 4.1 Difference in skid trail width (a) and rut depth (b) among the three stand types of STP30, STP50 and STP63.

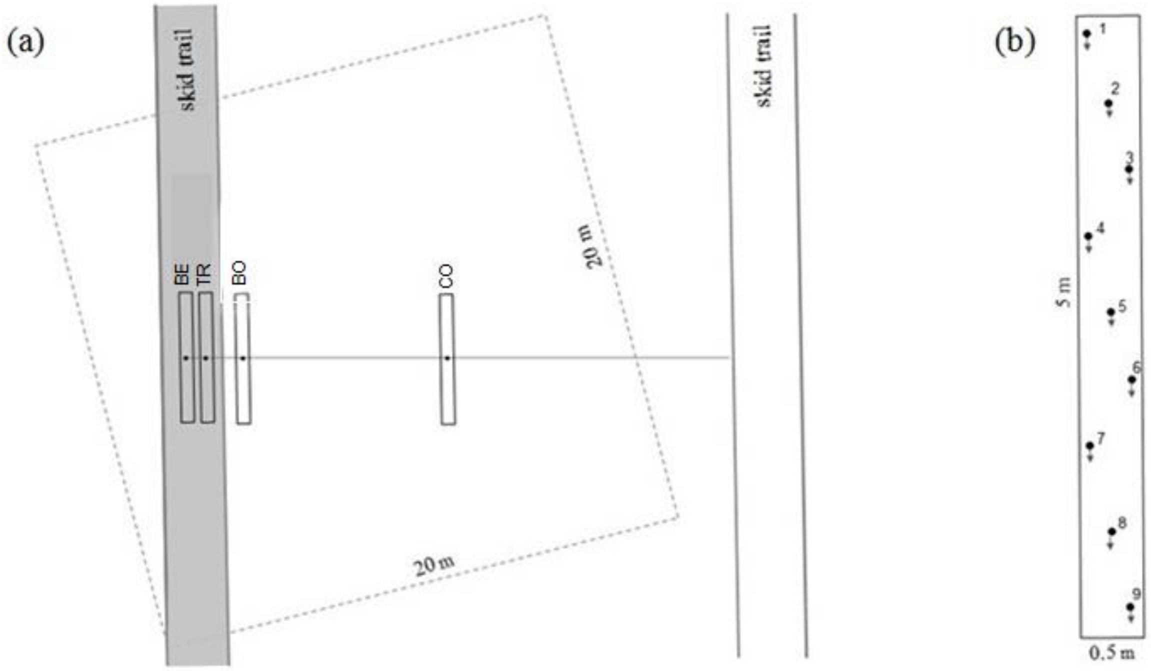


Figure 4.2 (a) Subplots setting (size: 0.5m × 5m) in 400m^2 quadrats. TR: on the wheel tracks of skid trail, BE: between the two tracks of a skid trail, BO: on the forest border next to the trail of a skid trail, CO: control, undisturbed habitat, at middle distance from the next parallel skid trail. (b) Fixed and numbered locations of PR spots. The number No. 1-9 represents the 9 measures of PRs, the arrows represent the direction of a renewed measure when the probing rod encountered stone or root above 20 cm soil depth. Bulk density sample was taken at No. 5.

Vegetation in each subplot was sampled once from May to end of July 2012. We may have underestimated vernal species occurrence and abundance. Yet only two vernal species (*Anemone nemorosa* and *Hyacinthoides non-scripta*) are present on the mildly acidic soils of the Montargis forest. Moreover, we were still able to detect these two species during our sampling season, although probably in reduced abundance. Vascular plants below 2m height were recorded in each subplot following the Braun-Blanquet abundance-dominance classification: i: one unique individual, cover < 5 %; +: very few individuals, total cover < 5 %; 1, few to many individuals, total cover < 5 %; 2, many individuals, total cover [5; 25 %[; 3, total cover [25; 50 %[; 4, total cover [50; 75 %[; 5, total cover > 75 %. When calculating species abundance, the abundance-dominance coefficients (i, +, 1, 2, 3, 4 and 5) were transformed into the following respective cover percentages: 0.1, 0.5, 5, 17.5, 37.5, 62.5 and 87.5%.

Soil compaction degree was assessed in each subplot from both penetration resistance (PR) and bulk density (BD) measures done at the same time in November 2012. At that period, the soil was near field capacity in Montargis forest, so that penetrometer readings are least influenced by differences in soil moisture (Wolkowski and Lowery; Miller et al., 2001; Godefroid and Koedam, 2004). We made nine PR measures per subplot. The locations of PR spots were fixed and numbered (No. 1-9) as in Fig. 4.2 (b). Moisture at soil surface was measured simultaneously at the same 9 spots as PR by using a field tetra probe. PR (MPa) was recorded at 1 cm depth intervals when continuously (2 cm/s speed) inserting into soil the bipartite probing rod (with a cone-shaped tip of 60 degree and 1 cm² basal area surface) of the penetrologger (Eijkelkamp Agrisearch Equipment, the Netherlands) until it stopped due to high soil compaction or encountering root or stone. The maximum measuring depth of penetrologger is 80 cm. In case the probing rod stopped less than 20 cm belowground, we made additional measures (up to four times at most) in a fixed direction and distance (10 cm) from the original spot until it reached 20 cm depth at least (Fig. 4.2 (b)). We also recorded the number of times we had to renew the measure (Nsam). The mean PR of the nine sampling spots at 0-20cm depth was used as a proxy for soil compaction level for each subplot (Fig. 4.2 (b)). We took PR values at 0-20 cm depth because in previous studies, the strongest soil impact on ground vegetation appeared in this upper layer (Greacen and Sands, 1980; Ampoorter et al., 2007). Furthermore, this layer is also generally unaffected by the natural compaction in deeper soil (Godefroid and Koedam, 2004). The mean number of PR measurements and mean maximum depth of the nine sampling spots were also calculated as alternative proxies for soil compaction. For the samples that have two sets of PR values because of the renewed measures, we only kept the PR and maximum depth value from renewed one (that had the maximum depth of at least 20 cm depth). The mean soil moisture of the nine sampling spots was calculated to represent the moisture level of each subplot.

We took one bulk density sampling in the center (the same spot as No.5 of PR) of each subplot at depth of 7.5 cm to 12.5 cm, using metallic cylinders with 5 cm diameter and 5 cm height. At 10-cm-depth horizon of soil profile, we inserted the whole cylinder into the soil and then removed it carefully, trimmed the soil from the top or around the edges of the cylinder so that the volume of the soil was the same as that of the cylinder. We weighted the fresh mass of each sample in the lab (the day of soil collection), as well as the dry mass after

48 hours in the oven (105 °C). Bulk density and water content were calculated following the two following formulas:

$$BD = \frac{M_{dry}}{V_b}$$

$$\theta = \frac{M_{wet} - M_{dry}}{V_b \times \rho_w}$$

where *BD* is soil bulk density (g/cm^3), M_{dry} is the mass of dry soil (g), V_b is the volume of the cylinder (cm^3), θ *is the* volumetric water content (cm^3/cm^3), M_{wet} is the mass of the sample before drying in the oven (g), ρ_w is the density of water (g/cm^3).

We used four indicators of soil compaction degree as we felt that none was unambiguously more appropriate than the others: mean PR of 0-20 cm depth (PR), mean number of measurements (Nsam) of each PR spot, maximum depth (MaxD) and bulk density (BD). Nsam can be a useful predictor of compaction degree (the higher Nsam, the more compacted the soil), although its relevance has never been tested so far. The maximum depth the bipartite probing reached (MaxD) decreases with increasing soil compaction and could reflect soil conditions for plant root penetrations. Though PR measurement is tenfold more sensitive to soil compaction variation than BD sampling (Vazquez et al., 1991), we still used BD as one of the variables because relationship between PR and BD were not always consistent and were found to be non-linear in some studies (Henderson et al., 1988; Smith et al., 1997; Vaz et al., 2001; Whalley et al., 2005; Ampoorter et al., 2007). Furthermore, the use of only one of these variables may lead to misleading results (Campbell and Henshall, 1991), because bulk density is more related to natural soil characteristic such as texture, organic matter, soil structure (Cassel, 1982) and gravel content (Franzen et al, 1994), while PR attempts to mimic a root growing through soil. Among the 36 sampling plots, we selected 24 ones (8 per stand type, randomly distributed in the forest) for light measurement in September 2013 when leaves were fully developed. The light transmission of subplots was measured for 24h using SKP215 (Skye Instruments) sensors in the photosynthetically active radiation spectrum (PAR, 400–700 nm, in $\mu mol.m^{-2}.s^{-1}$) (Balandier et al., 2008). We set one sensor 2m high above the center of each subplot and a control sensor in an open area nearby (hemisphere free of any obstruction) to measure incident radiation. Considering the varied diffused radiation due to weather conditions, we also set a sunshine sensor (Delta-T Devices) in the open area to assess the diffused radiation. Hemispherical photographs were taken to compute the precise time of sunset and sunrise above the tree periphery for each sampling day (Adam et al, 2008). Light transmittance of each subplot was calculated as the ratio between daily mean PAR and daily mean incidence radiation. Light data from sunset to sunrise was omitted. The ratio of diffused to incident radiation was used to correct daily mean PAR data: $PAR_{correct} = PAR \times (1\text{-}(\text{diffused radiation}/\text{incident radiation}) \times 0.15$. This process enabled us to compare measurements made on different days (i.e., with different sun fluxes) and with different weather conditions (i.e., cloudy or sunny) (Balandier et al., 2008). Relative PAR value (PAR value of each subplot divided by full light PAR) was finally calculated as light availability indicator.

4.3.3 Data analysis

We assessed the association between different soil compaction indicators (PR, Nsam, MaxD and BD) with correlation tests and the variation of soil compaction, soil moisture and light among subplot locations and stand types, using generalized linear model (GLM) with the Poisson "family". We then modeled the responses of ecological groups (in terms of richness and abundance, table 4.1) and individual species (in abundance for species with occurrence > 25 %) to variables that related to subplot location, soil compaction degree, stand attributes, soil moisture or light (Table 4.2). The variables (Table 4.2) were put in different generalized linear mixed models (GLMM) for coefficient estimation and model comparison with QAICc with a common dispersion parameter for all the models being compared (Bolker et al., 2009). The lmer function (in the lme4 R package, with the default Laplace approximation to the loglikelihood) with the Quasi-Poisson "family" was used. The link function was the default (log) for these models. A random "plot" effect was incorporated on the intercept into all the models in Table 4.3. The common dispersion parameter for model comparison through the QAICc (Table 4.4 and 4.5) was taken to be that of the Quasi-Poisson model: PR + STP (with STP stand type; see Table 4.3 for a definition of this model).

The classification of ecological groups were based on four species traits as follows (Table 4.1): life form, seed bank strategy, light and moisture requirements (data source: Julve, 2007; Hodgson et al., 1995). Relationships between ecological or functional groupings of plant species and environmental gradients can provide evidence for environmental filtering, particularly when the traits suggest an advantage in the associated environment (McGill et al., 2006; Burton et al., 2011)**.** Tree regeneration on skid trails was often investigated in previous studies. Seed bank was considered to be an important potential seed source for the restoration of plant communities (Bakker & Berendse 1999). It has been shown to be related to the ground vegetation response to skid trails (Roovers et al., 2004; Godefroid and Koedam, 2004). Light and moisture requirements are also basic plant traits widely used in studies of ground flora diversity (Brockerhoff et al., 2003; Jennife et al., 2005; Fierke and Boone Kauffman, 2005).

Table 4.1 Summary of ecological groups

Species trait	Categories	Description
Life form	Tree	
	Shrub	
	Herb	
Seed bank persistence	Transient	1: present during the summer and germinating synchronously in autumn, 2: present during the winter and germinating synchronously in late winter or spring
	Short-term persistence	3 : >5 years but concentrations of seed in the soil are only high after seed has just been shed
	Long-term persistence	4: a large bank of long persistent seeds in the soil throughout the year
Light	Shade-toelrant	Ellenberg L value : 2, 3, 4
	Heliophilous	Ellenberg L value : 5, 6, 7, 8
Soil moisture	Low-moisture	Ellenberg F value : 4
	High-moisture	Ellenberg F value : 5, 6, 7, 8

Table 4.2 Ecological variables used in the models

Variable	Description	Mean / SD
Subplot.location	Subplot location: BE: between the two tracks of a skid trail, TR: on the track of skid trail, BO: on the forest BO next to the trail of a skid trail, CO: control, undisturbed habitat, in the middle of two parallel skid trails)	---
STP	Stand type: 3 even-aged high forests stand types of mean age 30, 50 and 63 years (STP30, STP50, STP63) (year)	---
G	Basal area at breast height of total tree stands (m^2/ha)	28.21 / 6.41
PR	Mean penetration resistance of 0 to 20 cm depth (MPa)	1.95/ 0.66
Nsam	Number of PR measures per subplot (proxy for stone and root density)	1.34/ 0.81
Moisture	Soil moisture (%)	23.58 / 6.47
BD	Bulk density at 10 cm depth (g/cm^3)	1.07 / 0.26
WCS	Water content of BD (cm^3/cm^3)	19.58 / 5.95
L	Relative photosynthetic active radiation PAR value (%)	1.84/1.91
MaxD	Maximum depth (cm)	47.33 / 10.45

Table 4.3 Summary of ecological models

Effect	Models
	[1] Null model
Single-variable models	[2-11] Subplot.location, STP, G, PR, MaxD, Nsam, moisture, BD, WCS, L
Interactive models	[12] subplot.location * STP [13] subplot.location * G
Additive models	[14] PR + STP [15] MaxD + STP [16] Nsam + STP [17] BD + STP [18] Moisture + STP [19] WCS + STP [20] L + STP
Quadratic models	[21] PR + PR^2 + STP [22] MaxD + $MaxD^2$ + STP [23] Nsam + $Nsam^2$ + STP [24] Moisture + $Moisture^2$ + STP [25] BD + BD^2 + STP [26] WCS + WCS^2 + STP [27] L + L^2 + STP

We defined 27 models in total (Table 4.3). All these models were applied to each ecological group (10 groups) and individual species (9 species). Our first group of ecological models was single-variable models related to subplot location, stand type, basal area, soil compaction degree (PR, MaxD, Nsam, BD) and light (models [2] to [11]). The comparison of the single-variable models helps us distinguish the dominant factor on skid trails. To further detect whether ground flora diversity patterns could be better explained by the combined effects of subplot location, soil moisture, soil compaction or light with stand type or basal area, we modeled the interactive effects of subplot location and stand attributes (stand type and basal area) in the second group (models [12] and [13]), as well as the additive effects of soil compaction degree, soil moisture or light and stand type in the third group (models [14] to [20]). The four soil compaction variables (PR, Nsam, MaxD and BD) were put in parallel models from model [14] to [17]. The last group of models included quadratic models related to soil compaction degree, soil moisture and light (models [21] to [27]), since in several studies non-linear relationship between PR and plant species cover were detected (Godefroid and Koedam, 2004). Models related to light (models [11], [20] and [27]) were not compared directly with the other models since light was not measured in all plots. Only on the 24 plots on which light measurement was available, we compared light models only with the best ones selected from the other 26 model (Table 4.6 and 4.7).

Analyses based only on *P*-values are unable to distinguish practically important different situations in 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 tell whether the trend is ecologically important. The important question is actually whether the true trend is ecologically negligible or not (Dixon and Pechmann, 2005). As Barbier et al., (2009) did, we distinguished more stringent (b_1) and less stringent (b_2, with ($0 < b_1 < b_2$)) negligibility intervals for both richness and abundance data to define two equivalence regions that include all values of the trend parameters that are ecologically negligibility (very weak for b_1 and weak for b_2). Three different cases occur when describing negligibility effects: (1) weak and very weak effects, respectively denoted by “0” when the value of the multiplier (denoted by β) follows $P(-b_2 < \log(\beta) < b_2) \geq 0.95$ and “00” for the more stringent: $P(-b_1 < \log(\beta) < b_1) \geq 0.95$; (2) negative and very negative effects: “-” for $P(\log(\beta) < -b_1) \geq 0.95$ and “- -” for the stronger: $P(\log(\beta) < -b_2) \geq 0.95$; (3) positive and very positive effects: “+” for $P(\log(\beta) > b_1) \geq 0.95$ and “++” for the stronger:

$P(\log(\beta) > b_2) \geq 0.95$. In our analysis, we chose $b_1 = 0.1$, $b_2 = 0.2$ for species richness, and $b_1 = 0.25$, $b_2 = 0.5$ for abundance as in Barbier et al., (2009). That is, we considered that a change of $\exp(0.1) \approx 1.11$ in species richness (or $\exp(0.25) \approx 1.28$ in abundance) was a - ecologically - significant change, while a change of $\exp(0.2) \approx 1.22$(or $\exp(0.5) \approx 1.65$ in abundance) was a strongly significant change (see Table A1 in Appendix).

We analyzed the magnitude of the effects of the best models (lowest QAICc) on the richness and abundance of each ecological group, as well as the abundance of each species (occurrence > 25%). The bootstrap resampling method of R boot library was used to estimate the confidence intervals of the estimators of the models, at both the ecological group and species levels based on 10,000 simulations (Efron and Tibshirani, 1986; Hall et al., 1990). The bootstrap method resamples the original data with replacement, calculates the index of interest from each bootstrap sample, and estimates the mean, confidence interval and standard error from the replicate bootstrap estimates (Mueller and Altenberg, 1985; Krebs, 1989; Labropoulou and Eleftheriou, 1997). For each bootstrap sample, the multiplicative coefficient of the mean fitted value for richness and abundance data were calculated, to estimate the response of ground flora to the numerical increase in the variables. A variable would have a - ecologically - significant effect if an increase of one SD (standard deviation) for a continuous variable is related to a 1.11-time increase/decrease in richness (or 1.28 in abundance) (cf. Table 4.8). The increase in the variables of about one standard deviation were: 0.5 MPa for increment for PR, 1 for Nsam, 10.5 cm for MaxD, 0.25 $g.cm^{-3}$ for BD, 6.5 % for moisture, 6 $m^3.cm^{-3}$ for water and 5 $m^2.ha^{-1}$ for basal area. For stand type (STP), we calculated the associated multiplicative coefficient by supposing the stand changed from one type to the next successive type: STP30 to STP50 stands (STP_{30to50}), and STP50 to STP63 stands (STP_{50to63}). The multiplicative coefficient for subplot location was obtained by calculating the difference between the subplot locations and control (BEtoCO, TRtoCO and BOtoCO). For quadratic models, we obtained the multiplicative coefficient for the same variation as above but calculated at first, second and third quartile of the explanatory variable. We reported the mean value of the multiplier for each variable and its 95% confidence interval.

4.4 Results

4.4.1 Fine-scale variation of environmental factors

PR was significantly greater on wheel tracks (TR) than on controls in STP50 and STP63 and between the two wheel tracks (BE) in STP63 (Fig. 4.3). Nsam and BD were also significantly higher on TR in STP63. PR, Nsam and BD on the subplot location of BE and TR increased with the increasing age of high stands. No significant variation in MaxD among subplot locations was detected (Fig. 4.3). BD, Nsam and MaxD significantly associated to PR (*$P<0.001$*). Light and soil moisture did not vary among subplot locations whatever the stand type (Fig. 4.4), but varied among stand types (*$P<0.001$*).

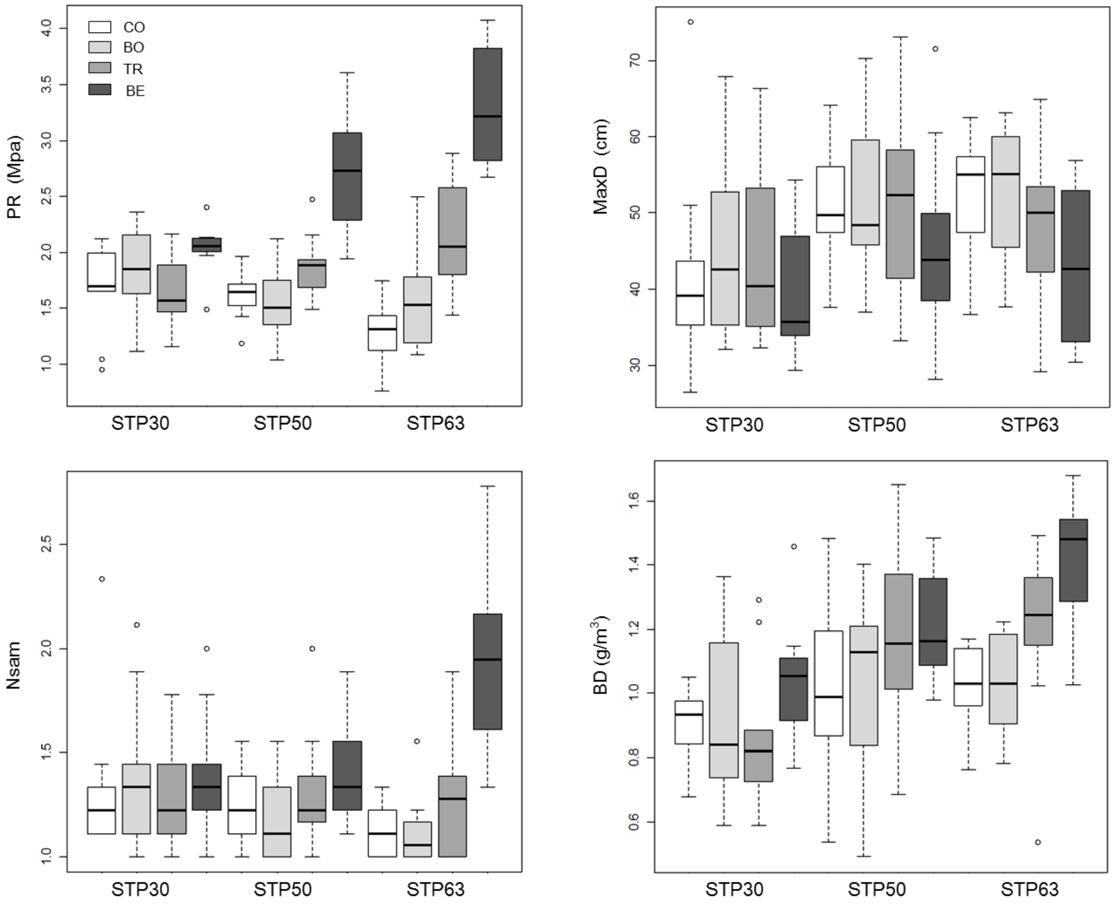


Figure 4.3 Distribution of PR, MaxD, Nsam and BD depending on subplot locations (CO, BO, TR and BE) and stand type (STP30, STP50 and STP63). TR: on the TR of skid trail, BE: between the two tracks of a skid trail, BO: on the forest BO next to the trail of a skid trail, CO: undisturbed habitat, in the BE of the two parallel skid trails).

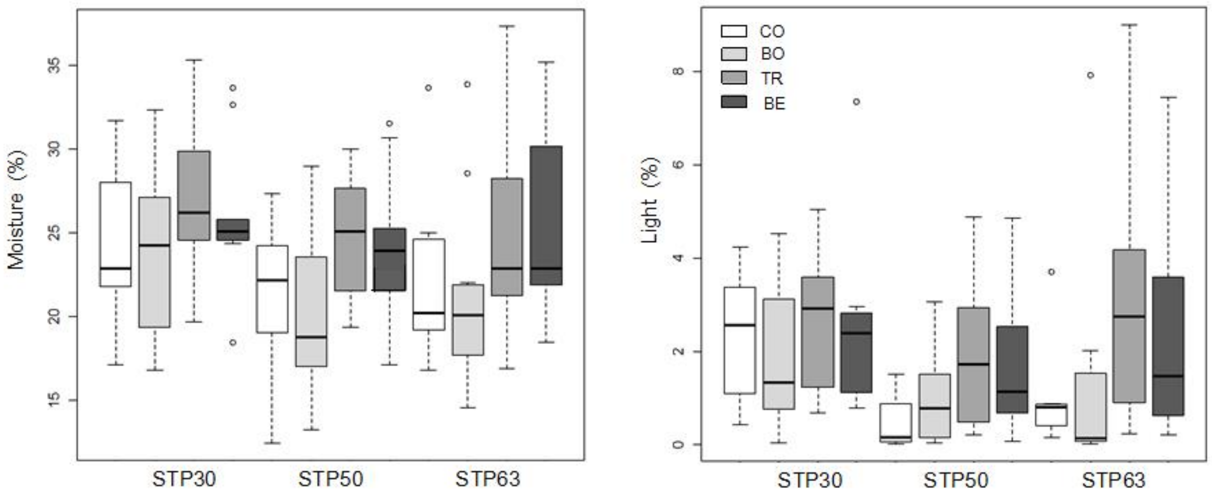


Figure 4.4 The distribution of moisture and light in each subplot locations (CO, BO,TR and BE) in the three stand types of STP30, STP50 and STP63. TR: on the TR of skid trail, BE: between the two tracks of a skid trail, BO: on the forest BO next to the trail of a skid trail, CO: undisturbed habitat, in the BE of the two parallel skid trails).

4.4.2 Ecological group level

The best models fell into two broad categories (Table 4.3): models related to subplot location that indirectly represent the disturbance gradient and models related to micro-site factors of soil compaction degree, soil moisture or light. Among the total 10 ecological groups, for richness, 2 groups (tree and short-term seed bank species) had their best models related to the interactive effects of subplot location and stand type, 4 groups (herb, shrub, long-term seed-bank and heliophilous species) were best related to soil compaction indices (PR, MaxD or BD) and 4 groups (transient seed bank, high-humidity, low-humidity and shade-tolerant species) to soil moisture (Table 4.4). For abundance data, 3 groups (long-term seed bank, high-humidity, shade-tolerant) had their best models that related to subplot location, 3 groups (tree, shrub, and heliophilous) related to the interactive of subplot location and basal area, 2 group related to PR (shrub, transient seed-bank) and 2 groups related to soil moisture (herb and short-term seed bank) (Table 4.5). Light-only (L) models were preferred to alternative models for the richness of heliophilous species and the abundance of long-term seed-bank species (Tables 4.6 and 4.7). Models combining light and stand type (linear and quadratic models) were the best for the richness of herb species.

For richness data, the magnitude and negligibility of the effects estimated from the best models are shown in Tables 4.8 and 4.10. Subplot locations of BE and TR had positive effects on tree and short-term seed bank species in STP50, which was the same case for the subplots of BE, TR and BO on tree and short-term seed bank species in STP63. Soil moisture showed positive effects on the richness of all the ecological groups which had best models related to soil moisture (transient seed bank, low-humidity, high-humidity and shade-tolerant species). For compaction indicators, BD had a positive effect on heliophilous species richness. The effect of MaxD was either weak (long-term seed bank species) or uncertain (shrub). PR effect was also weak (herb). The effect of light was either weak (herb) or uncertain (heliophilous).

The transition of stand type from STP30 to STP50 had negative effect on shrubs in the additive models of MaxD and STP, while it had positive effect on herb richness in the additive models of PR and STP. The transition of stand type from STP50 to STP63 had positive effect on herbs in the model combining light and stand type, while it was weak for herb and uncertain for shrub.

Table 4.4 Differences in QAICc values between the different ecological models and the null model for the richness of the ecological groups

Models	Lifeform			Seed bank			Humidity		Light	
	Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot.location	-36.54	4.25	2.98	3.10	-44.83	0.01	-0.44	-11.38	-18.57	-13.45
STP	-1.87	-7.23	-23.98	1.04	-1.62	2.20	-1.32	3.20	3.72	-7.49
Subplot * STP	**-37.76**	8.12	-10.01	15.56	**-55.54**	10.95	-0.26	4.45	-4.57	-16.12
G	0.89	-1.51	1.96	0.92	1.90	0.71	1.13	-0.19	0.47	1.08
Subplot * G	-31.66	7.41	9.86	7.25	-37.35	4.29	7.18	-10.30	-12.08	-8.35
PR	-13.91	-0.65	1.03	1.40	-48.22	1.59	1.19	-1.87	-8.85	-2.91
PR + STP	-16.87	-6.78	**-24.67**	2.82	-50.37	3.98	-0.72	1.56	-4.65	-11.57
MaxD	-3.37	-0.35	-1.86	-0.18	-11.52	1.93	0.49	2.13	1.50	-0.13
MaxD + STP	-2.94	**-12.06**	-22.16	2.14	-10.85	3.64	0.48	5.39	5.10	-5.67
Nsam	-0.90	-3.34	1.39	2.04	-14.78	-0.23	2.05	2.09	1.33	1.74
Nsam + STP	-2.18	-11.76	-22.29	3.20	-14.84	1.60	0.70	5.39	5.17	-5.45
Moisture	-32.33	1.98	1.75	1.85	-32.28	**-11.80**	**-11.08**	**-13.98**	**-23.26**	-11.63
MoisturePR + STP	-31.01	-5.19	-21.93	2.36	-31.54	-8.09	-10.58	-10.56	-20.85	-16.04
BD	-15.58	1.32	-0.71	2.09	-24.76	-0.85	-3.66	-7.30	-13.81	**-18.00**
BD + STP	-22.71	-5.09	-21.78	3.07	-30.73	-0.39	-10.39	-4.92	-9.91	-5.24
WCS	-5.47	1.44	0.41	2.13	-5.15	-2.98	-2.50	-1.76	-9.46	-0.24
WCS + STP	-9.15	-5.19	-23.74	3.19	-9.12	-2.21	-5.28	0.49	-6.69	-9.03
PR + PR^2 + STP	-31.02	-6.17	-19.71	4.58	-33.65	-8.93	-9.71	-1.41	-5.09	-11.96
BD + BD^2 + STP	-21.19	-2.95	-19.58	5.25	-28.92	1.82	-8.19	-2.93	-7.68	-15.81
Moisture + Moisture^2 + STP	-31.02	-6.17	-19.71	4.58	-33.65	-6.14	-8.79	-10.06	-22.84	-14.34
WCS + WCS^2 + STP	-6.32	-4.48	-21.51	5.23	-7.24	-0.03	-7.54	2.60	-4.52	-7.17

The detailed information about ecological groups can be found in Table 4.1, and the mean of ecological variables in Table 4.2. Within each ecological group, the model with the smallest QAICc at least 5 units below the null model is in bold and the QAICc values within 5 units of this model are underlined.

Table 4.5 Differences in QAICc values between the different ecological models and the null model for the abundance of the ecological groups

Models	Lifeform			Seed bank			Humidity		Light	
	Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot.location	-36.38	-3.31	-38.31	**-11.61**	-21.26	-20.23	0.80	**-20.11**	**-29.88**	-13.28
STP	3.71	4.29	-1.71	3.77	2.51	4.22	3.83	4.28	4.20	3.55
Subplot * STP	-31.90	-3.20	-34.74	-3.88	-7.34	-13.42	9.80	-10.25	-20.50	-13.75
G	2.10	1.63	1.97	1.84	2.10	2.10	2.21	2.08	2.11	2.10
Subplot * G	**-37.66**	-6.20	-35.28	-4.46	-16.73	-15.53	5.02	-18.35	-25.71	**-15.66**
PR	-1.16	**-6.81**	-29.48	1.33	-13.20	-18.40	**-7.17**	1.85	-17.03	0.65
PR + STP	2.58	-2.41	-31.28	5.20	-10.82	-14.08	-3.10	6.20	-13.00	4.30
MaxD	0.38	-6.66	-15.34	1.70	0.05	-3.31	2.13	1.81	-6.40	0.89
MaxD + STP	4.28	-2.67	-14.97	5.58	3.10	0.83	6.02	6.16	-2.19	4.38
Nsam	-1.03	2.06	-21.46	2.00	-15.02	-6.45	-2.60	2.13	-12.45	1.57
Nsam + STP	2.77	6.44	-22.79	5.85	-11.86	-2.18	1.22	6.48	-8.34	5.18
Moisture	-18.63	-0.68	-6.03	1.44	**-22.72**	2.12	1.36	-5.24	-28.99	-0.95
MoisturePR + STP	-14.67	3.64	-6.34	5.20	-19.40	6.41	5.49	-0.95	-25.03	2.75
BD	-4.13	-4.84	-2.31	1.86	-5.86	1.67	-1.83	0.73	-20.26	1.91
BD + STP	-0.59	-0.52	-4.22	5.74	-4.00	5.99	2.54	5.08	-16.36	5.48
WCS	-1.97	-3.78	2.07	2.10	-3.97	1.70	1.79	-0.74	-2.44	1.28
WCS + STP	1.76	0.44	0.42	5.94	-1.97	5.98	5.68	3.60	1.97	4.88
PR + PR^2 + STP	-1.22	-2.34	-4.95	4.98	-8.66	**-26.24**	-1.19	-1.82	-18.63	2.06
BD + BD^2 + STP	-1.40	-0.68	-6.06	2.01	-2.29	6.29	0.03	5.02	-14.75	1.32
Moisture + Moisture^2 + STP	-12.94	0.87	**-97.68**	7.45	**-22.64**	8.48	7.84	0.84	-25.86	4.68
WCS + WCS^2 +STP	3.81	2.53	2.65	8.19	-1.85	6.47	8.83	3.95	4.24	7.11

The detailed information about ecological groups were in Table 4.1, the mean of ecological variables were in Table 4.2. Within each ecological group, the model with the smallest QAICc at least 5 units below the null model is in bold and the QAICc values within 5 units of this model are underlined.

Table 4.6 Differences in QAICc values between the best models and models related to light for the richness of the ecological groups

	Lifeform			Seed bank			Humidity		Light	
	Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot + STP	**-30.39**				**-44.50**					
PR + STP			**-23.64**							
MaxD				-0.26						
MaxD + STP		**-15.43**								
Moisture						-4.64	-2.73	-3.97	**-18.29**	
Moisture + STP										
BD + STP										42.04
L	-11.34	-0.24	-0.05	2.15	-15.80	0.69	0.41	-3.61	-9.95	**-9.17**
L + STP	-10.33	-9.65	**-23.65**	6.54	-13.00	4.57	-0.85	-1.70	-5.89	-5.08
L + L^2 + STP	-9.16	-7.35	**-23.75**	8.30	-14.60	6.36	1.34	0.65	-6.22	-5.23

Table 4.7 Differences in QAICc values between the best models and related to light for the abundance of the ecological groups

	Lifeform			Seed bank			Humidity		Light	
	Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot			**-12.62**	-1.94				**-10.37**	**-37.8**	
PR + G	**-19.82**	-3.15								-2.23
PR		-2.65					1.45			
PR + PR^2 + STP						**-17.57**				
Moisture					**-13.07**					
L	-8.88	0.46	-4.38	**-7.08**	2.18	1.96	1.85	-0.45	-26.7	-0.19
L + STP	-4.75	4.86	-4.33	-2.71	7.16	6.40	6.07	3.95	-22.9	3.93
L + L^2 + STP	-5.03	7.19	-7.26	-1.72	9.26	3.99	8.67	6.12	-22.5	4.64

Table 4.8 Multiplicative effect of a substantial variation in ecological variables on the richness of the ecological groups

Models	RI	Lifeform			Seed bank			Humidity		Light	
		Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot* STP	BOtoCO, STP30	0.84 [0.54;1.25]				0.47 [0.16;2.51]					
	TRtoCO, STP30	1.13 [0.78;1.59]				1.20 [0.57;2.83]					
	BEtoCO, STP30	1.19 [0.81;1.68]				1.24 [0.54;2.48]					
	BOtoCO, STP50	1.01 [0.64;1.49]				0.99 [0.29;3.70]					
	TRtoCO, STP50	1.49^{+} [1.05;2.27]				2.69^{++} [1.13;7.95]					
	BEtoCO, STP50	1.68^{++} [1.20;2.48]				2.52^{+} [0.95;7.04]					
	BOtoCO, STP63	1.63^{++} [1.16;2.52]				3.95^{+} [0.86;9.96]					
	TRtoCO, STP63	2.39^{++} [1.74;3.63]				14.67^{++} [4.62;30.34]					
	BEtoCO, STP63	2.36^{++} [1.77;3.46]				8.91^{++} [2.92;19.57]					
MaxD	MaxD				1.06^{0} [0.98;1.15]						
	MaxD		1.16 [1.03;1.29]								
MaxD + STP	STP30to50		0.59^{--} [0.45;0.76]								
	STP50to63		1.10 [0.86;1.4]								
Moisture	Moisture						1.15^{+} [1.09;1.24]	1.51^{++} [1.25;1.80]	$1.17^{+,0}$ [1.11;1.23]	1.60^{++} [1.35;1.78]	

PR + STP	PR	0.96^{00} [0.93;1.00]	
	STP30to50	1.44^{+} [1.16;1.77]	
	STP50to63	1.11^{0} [1.01;1.22]	
BD	BD		1.11^{+} [1.11;1.27]

Variations were: an addition of 0.5 MPa for PR, 1 for Nsam, 10.5 cm for MaxD, 0.25 g.cm^{-3} for BD, 6.5 % for moisture, 6 m^{3}.cm^{-3} for water and 5 m^{2}.ha^{-1} for basal area. For stand type (STP), we calculated the associated multiplicative coefficient by supposing the stand changed from one type to the next successive type: STP30 to STP50 stands (STP30to50), and STP50 to STP63 stands (STP50to63). The multiplicative coefficient for subplot location was obtained by calculating the difference between the subplot locations and control (BEtoCO, TRtoCO and BOtoCO). “0” and “00” indicate that the effect has a *p*-value of at least 0.95 of being negligible at two different levels (see text). “$^{-}$” and “–” indicate that the effect has a *p*-value of at least 0.95 of being negative and non-negligible at two different levels. “$^{+}$” and “$^{++}$” indicate that the effect has a *p*-value of at least 0.95 of being positive and non-negligible at two different level. Values in brackets are 95% confidence intervals of the coefficients.

Table 4.9 Multiplicative effect of a substantial variation in ecological variables on the abundance of the ecological groups

Models	RI	Lifeform			Seed bank			Humidity		Light	
		Tree	Shrub	Herb	Long-term	Short-term	Transient	Low	High	Shade	Heliophilous
Subplot.location	BOtoCO				1.16^{0} [0.82;1.67]				1.30^{0} [1.04;1.62]	1.16 [0.51;2.27]	
	TRtoCO				1.28 [0.9;1.77]				1.22^{0} [0.96;1.54]	2.75+ [1.25;4.6]	
	BEtoCO				1.65 [1.16;2.39]				1.51 [1.22;1.86]	2.35 [1.12;3.95]	
Subplot * G	BOtoCO	1.34^{0} [0.91;1.70]									1.31^{0} [0.9;1.7]
	TRtoCO	1.63 [1.14;2.02]									1.25^{0} [0.84;1.6]
	BEtoCO	1.95^{+} [1.3;2.4]									1.62 [1.1;2.03]
	BO.G	1.14^{0} [0.89;1.43]									1.15^{0} [0.91;1.46]
	CO.G	0.84^{0} [0.60;1.16]									0.83^{0} [0.59;1.16]
	BE.G	1.15^{0} [0.95;1.45]									1.15^{0} [0.95;1.45]
	TR.G	1.59^{00} [0.87;1.26]									$1.10^{00,0}$ [0.89;1.33]
PR	PR		2.20++ [2.15;2.68]					0.72 [0.50;0.95]			
Moisture	Moisture					3.21^{+} [1.41;7.16]					
Moisture+Moisture^{2}+STP	Moisture at 1st quartile			0.93^{00} [0.81; 1.10]							

	Moisture at median	0.86^{00} [0.79;0.96]	
	Moisture at 3rd quartile	0.81^{0} [0.72;0.88]	
	STP30to50	4.35^{++} [2.53;6.25]	
	STP50to63	1.01^{0} [0.81;1.31]	
PR+PR^2+STP	PR at 1st quartile		1.00^{00} [0.92;1.12]
	PR at median		0.91^{00} [0.84;0.98]
	PR at 3rd quartile		0.83^{0} [0.75;0.92]
	STP30to50		0.93^{00} [0.78;1.16]
	STP50to63		1.11^{0} [0.91;1.34]

The legend is the same as for Table 4.6.

Table 4.10 Multiplicative effect of a substantial variation in ecological variables (in the models related to light) on the richness and abundance of ecological groups

		Richness		Abundance
Models	Variables	heliophilous	herb	Long-term seed bank
L	L	1.15 [1.01;1.26]		1.18^{0} [1.05;1.34]
L + STP	L		0.98^{00} [0.93;1.01]	
	STP30-50		1.54^{+} [1.20;2.00]	
	STP50-63		1.16 [1.03;1.31]	
$L+L^2+STP$	L at 1st quartile		0.94 [0.88;1.00]	
	L at median		0.95 [0.89;1.01]	
	L at 3rd quartile		0.96^{0} [0.90;1.01]	
	STP30-50		1.50 [1.17;1.97]	
	STP50-63		1.14^{+} [1.00;1.29]	

For abundance data (Table 4.9 and 4.10), TR and BE had positive effect on shade-tolerant and tree species respectively. Soil moisture had positive effect on short-term seed bank species, whereas its effect on herbs was weak. Similarly, PR had a positive effect on shrubs, a weak effect on transient seed bank species, and its effect on low-humidity species was uncertain. The effect of light was weak (long-term seed bank). The transition of stand type from STP30 to STP50 had positive effect on herbs and weak effect on transient seed bank species in the quadratic model combing soil moisture and stand type. The effects of the transition of stand type from STP50 to STP63 on herb transient seed bank species were weak. Basal area had either weak (trees and heliophilous species) or uncertain (shrubs) effect in the models combining subplot and basal area.

4.4.3 Species level

For the 15 species whose occurrence was more than 25%, 12 species had the best models related to subplot location (*Melica uniflora*, *Rubus fruticosus* and *Viola riviniana & reichenbachiana*) or the combined effects of subplot location and stand type/basal area (*Carpinus betulus, Carex pilulifera, Deschampsia flexuosa, Festuca heterophylla, Holcus mollis, Hypericum pulchrum, Poa nemoralis, Teucrium scorodonia* and *Potentilla sterilis*) (Table A2 in Appendix). The other three species (*Lonicera periclymenum*, *Hedera helix* and *Quercus sp*) had best models related to PR or Nsam. Models related to light were the best for the abundance of *Melica uniflora* and *Rubus fruticosus* and *Quercus sp* (Table A3 in Appendix). The results of the magnitude and negligibility analysis showed that TR, BE and BO in STP63 had positive effects on *Hypericum pulchrum* compared to control, and TR positively affected the abundance of *Festuca heterophylla*. In STP30, TR positively affected *Holcus mollis* and *Teucrium scorodonia.* The transition of stand type from STP30 to STP50 had positive effect on *Quercus sp* in the model combining effects of light and stand type, while the transition of stand type from STP50 to STP63 positively affected *Hedera helix* and *Quercus sp* in the model combining PR and stand type. The effect of PR on *Lonicera periclymenum* was weak and Nsam effect on *Quercus sp* was uncertain (Table A4 and A5 in Appendix).

4.5 Discussion

4.5.1 Best models for ecological groups and individual species

Disturbance, soil moisture, soil compaction, light, stand type and basal area variables have been found to be important factors impacting understory diversity (Nagaike et al., 2005; Nilsson et al., 2008; Sciama et al., 2009; Skov 1997; Barbier et al., 2009), but few studies compared the relative importance of these variables to detect which one(s) might be the best indicator(s) under the multiple hypotheses framework (Chamberlin, 1965). In our study we used model comparison approach to find out the best indicators of ground flora diversity. For the majority of ecological groups (8 out of 10 groups), the best indicators of species richness were related to micro-environmental factors, while the abundance of most groups (7 out of 10) was best indicated by models related to subplot location (Tables 4.4 and 4.5). The responses of the 15 species we studied were similar – being mainly affected by the models related to subplot location or its interactive effect with stand type or basal area (12 out of 15 species) (Table A2 and A2 in Appendix).

4.5.2 Responses of ecological groups and individual species to their best indicators

In our study, the species richness of tree seedling and sapling was higher on skid trails than in interior forest (Table 4.6). The positive role of skid trail on tree recruitment, growth and seedling density has already been repeatedly evidenced in previous studies (Swaine and Agyeman, 2008; Roberts and Harrington, 2008; Nakagawa and Kurahashi, 2005). A more innovative finding is that the positive influence of skid trails on tree species richness depended on forest type – higher richness on skid trails only occurred in oldest stands (50 and 63 year-old) but not in youngest stands (30 year-old) (Table 4.6). This is because with increasing stand age, the richness of tree seedling and sapling progressively decreased on controls but did not change on skid trails. For the other two life-form groups (shrubs and herbs), soil compaction has been found to respectively reduce the herb cover and to increase the shrub richness and cover in large plots ($60m^2$) (Zenner and Berger 2008). Our study also demonstrated a positive effect of soil compaction on shrub abundance at fine scale. Though the model combining soil compaction and stand type was the best for herb richness, it mostly showed a positive effect of ageing of trees (from 30 to 50 years) while the effect of soil compaction was weak.

Species producing a large number of persistent seeds (seed banks live for ≥1 year defined by Thompson and Grime, 1979) seem to be favored by recurring disturbance cycles, such as flooding, burning or tree falls, awaiting favorable conditions for germination in the soil (van der Valk & Davis 1978; Grime 1979; Pugnaire & Lázaro 2000; Czarneck 2004; Matus et al., 2005). As another form of recurring human-caused disturbance, skid trails were found to maintain higher diversity of species with short-term persistent seed bank (Avon et al., 2013), which is what we observed in stand aged of 50 and 63 years but not in younger stands. For transient seed bank species, the dominant factor affecting the richness of transient species was soil moisture rather than skid trail disturbance.

Concerning light demanding groups, Avon et al., (2013) found higher richness of shade-tolerant species in stand interior and more heliophilous species on skid trails. Conversely, Toledo-Aceves et al., (2009) emphasized that even shade-tolerant species displayed higher densities on skid trails in comparison with the closed canopy conditions. Higher abundance of shade-tolerant species on skid trails was also found in our study. For heliophilous species, bulk density was a better indicator than light or subplot location, having a positive effect on this group. Concerning ecological groups classified by soil moisture, no previous studies detected the effects of skid trails on moisture groups. We found that both the richness of both low- and high-humidity species increased with increasing moisture (Table 4.6).

At species level, subplot location was the only factor that showed significant effects on species abundance: *Holcus mollis* and *Teucrium scorodonia* had higher species abundance on tracks than on controls in the youngest stands, while the effect of subplot location in intermediate stands was uncertain. The confidence levels were very low at species level compared to that at group level, which might call for improved statistical models for species level analysis.

4.5.3 Dominant factors affecting ground flora diversity on skid trails

In our study, subplot location, soil moisture and soil compaction played dominant roles at fine scale in stands managed with skid trail system. The dominant effects depended on which ecological groups the species belonged to and on whether species richness or species abundance was considered. We agreed with Brosofske et al., (2001) that disturbance can sometimes override the environmental influences. Subplot location that indirectly represents disturbance gradient was the best indicator for the richness of tree and short-term seed bank species, as well as the abundance of tree species and shade-tolerant species. However, the effects of subplot location depended on stand types: its positive effects only occurred in the two older stand types. Skid trails in young stands were denser but narrower than in older stands, and were submitted to fewer and/or less intense disturbances. Indeed, soil compaction values on skid trails significantly higher than the paired forest controls were observed only in the two older stand types (Fig. 4.3). Furthermore, community stability reflects the ability of resident species to resist change, or, if altered by disturbance, their ability to readjust or recover (Halpern, 1988). By these criteria, the understory plant community in our research area appears to be resilient to the skid trail system. Skid trails did not appear to negatively impact ground flora diversity. On the contrary, it promoted the diversity of some ecological groups, as in Schumann et al., (2003).

Soil moisture was the best indicator for the richness of transient seed bank, shade-tolerant, low- and high- humidity species. In our study, soil moisture level significantly varied among stand types, whereas it did not vary along disturbance gradient in each stand type. Sattar Ezzati et al., (2012) got the similar finding that there was no moisture difference between skid trail and undisturbed forest 16-20 years after skidding operations. According to our results, both the richness of low- and high- humidity species were positively affected by soil moisture. The reason could be explained by Qian et al., (1997) that the trend of higher diversity in wetter soil conditions generally agrees with findings that diversity peaks at mesic sites (e.g. Burton et al., 1992; Pausas 1994; Roberts & Gilliam 1995a). Besides, in compacted habitats, soil moisture level may be wetter in spring, fall or winter but drier in summer than average level. This might favor both species with low and high soil moisture preference.

Our study supported the important role of soil compaction only for shrubs (with penetration resistance as the best indicator) and heliophilous species (with bulk density as the best indicator). Higher soil compaction detected on skid trails does not necessarily mean that it will have significant effects on ground flora. One reason may be that the soil compaction level in our study did not reach the level that may affect ground flora. This was supported by Zenner et al., (2007), who found that though traffic intensity had a negative effect on both aspen density and growth, penetration resistance (PR) measured from this traffic was not significantly associated with aspen density and growth. Zenner et al., (2007) explained that the PR values after harvest were below the levels that restrict suckering and growth of aspen. Specific PR values at which root growth is restricted are thought to be between 2,500 and 3,000 kPa for many plant species (Taylor et al., 1966, Greacen and Sands 1980). In our study, the critical value of 2,500 kPa was found only on the wheel tracks (TR) of stands aged of 50 and 63 years. Heninger et al., (2002) used bulk density as soil compaction indicator, and found that reductions in tree height were unrelated to percentage increases in soil bulk density in the 0 to 30cm soil horizon. Higher soil moisture was usually considered to result in more compacted soils (Siegel-Issem et al., 2005; McNabb et al., 2001; Williamson and Neilsen, 2000), and vice versa (Greacen and Sands, 1980; Tan et al., 2005). However, in our study, there was no strong relationship between penetration resistance and moisture (Pearson's r=0.148, *P*=0.0898). Besides, the effects of penetration resistance or moisture were only detected at group level but not at species level. More ecological groups were affected by soil moisture compared to soil compaction. Only one study to our knowledgecompared the effects of soil moisture and compaction at stand scale, and found that seedling growth rate in the periods 0–12 and 12–24 months after planting was promoted by higher soil moisture (33%), while penetration resistance had no effect (Hattori et al., 2013).

Light effect compared to control was weak in our study (Table 4.10). The study of Zenner et al., (2008) on plot covered with skid trails also failed to detect significant effects of canopy removal intensity on ground flora composition and diversity. Light did not vary among subplot locations in each stand type in our study. In fact, decades after the creation of skid trails, trees nearby are already tall enough so that the canopy cover can be fully developed even with disturbance. This was the case even in the youngest stands (30 years on average), because, although trees were relatively smaller and denser, the skid trails were narrower and the machines used were smaller than in older stands. Buckley et al., (2003) also found that mean canopy cover was just slightly lower on skid trails than in forest.

4.6 Conclusion

Our study compared the effects of disturbance and micro-environmental factors on ground flora diversity at fine scale. The interaction among the ecological factors and their relative importance on ground flora is summarized in Fig. 4.5. For the interaction among ecological factors (subplot, soil moisture, soil compaction, light and stand type), on the one hand, stands in different rotation stages had significantly different levels of light availability, soil moisture or soil compaction. On the other hand, among the three micro-environmental factors (light, soil moisture and compaction), only one factor - soil compaction - varied among subplot locations. Soil compaction was the only factor that was affected by skid trail disturbance, which was consistent with the previous studies that the recovery period of highly compacted soil could last decades or even more than a century.

Concerning the effects of the ecological factors on ground flora, we assessed their effects at both ecological group level and species level. Using model comparison method and negligibility analysis, dominant factors were subplot location, soil moisture and soil compaction. Disturbance indirectly represented by subplot location can override the environmental factors and was often the best indicator. At species level, subplot location was the only dominant factor affecting their abundance

In our study, skid trails had either no impact or a positive impact on ground flora diversity. We indeed found no negative effect of locations on skid trail on floristic diversity. Pickett (1980) noted that the persistence of certain species in plant communities requires disturbance. In particular, disturbances can significantly enhance ecological heterogeneity at multiple scales (White & Jentsch 2001; Schoennagel, Smithwick & Turner 2008; Mori & Lertzman 2011). However, in our research area, mechanized harvesting is relatively recent and harvesting practices with heavier machines is still likely to happen. Furthermore, given our study was conducted only in young stages of the forestry cycle (< 63 yr), further investigation on the skid trail effects in older stands is still needed. This is because, on the one hand, since we have detected an increasing trend of soil compaction with stand age, much higher levels of soil compaction and its impact on ground flora might be found during the maturing process of these stands; on the other hand, since light, soil moisture and compaction were detected to be vary among stand types, the relative role of these micro-environmental factors could be different in the older stands.

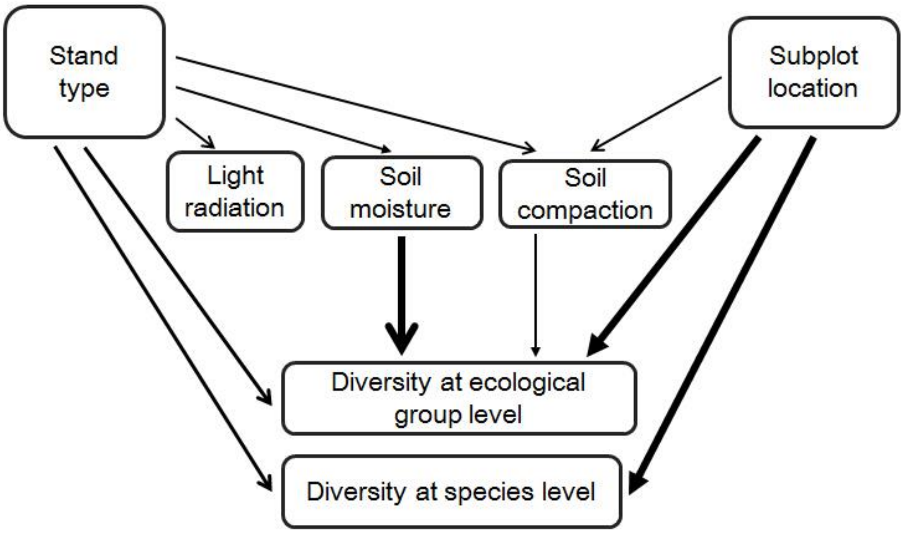


Figure 4.5 Summary of the interaction of different variables and their relative important roles on ground flora diversity. Boxes represent categories of variables, while the arrows show the relationships among categories and the directions of those relationships. Arrow width indicates relative importance of the pathway.

4.7 Appendix

Table A1 Different cases of describing negligibility effects of the variables

$\geq$ 95% probability		effects
richness	abundance	
$> \exp(0.2)$	$> \exp(0.5)$	strongly positive
$> \exp(0.1)$	$> \exp(0.25)$	positive
$\in [\exp(-0.2); \exp(0.2)]$	$\in [\exp(-0.5); \exp(0.5)]$	weak
$\in [\exp(-0.1); \exp(0.1)]$	$\in [\exp(-0.25); \exp(0.25)]$	very weak
$< \exp(0.2)$	$< \exp(0.5)$	strongly negative
$< \exp(0.1)$	$< \exp(0.25)$	negative
-	-	uncertain

Table A2 Differences in QAICc values between the different ecological models and the null model for the abundance of individual species

	Cabe	*Capi*	*Defl*	*Fehe*	*Hehe*	*Homo*	*Hypu*	*Lope*	*Meun*	*Pone*	*Post*	*Qusp*	*Rufr*	*Tesc*	*Vire*
Subplot.location	-20.16	-22.00	-5.90	-4.07	-23.91	-1.52	-14.09	-7.38	-15.12	-6.75	-51.67	-4.45	**-11.98**	-36.21	-95.32
STP	3.77	3.05	-2.10	3.32	0.75	-5.96	-4.45	4.14	3.69	2.43	1.97	-2.01	3.14	-9.81	0.63
Subplot * STP	**-38.01**	-31.40	**-33.14**	**-9.45**	-10.69	**-27.68**	**-71.49**	-10.81	-13.76	-36.40	-45.52	4.91	-5.14	**-52.90**	-86.85
G	1.66	0.64	2.09	2.10	2.10	2.08	2.09	1.55	2.12	1.95	-1.39	1.42	1.91	-1.34	-3.95
Subplot * G	-33.29	**-52.72**	0.16	-1.73	-17.01	0.42	-50.23	-11.29	-8.92	**-65.24**	**-59.72**	3.45	-3.66	-34.63	**-95.73**
PR	-14.04	-5.34	-2.13	-3.56	**-27.70**	-5.51	-26.08	-16.36	-6.66	2.07	-18.97	-3.98	1.67	-5.75	-15.83
PR + STP	-10.22	-2.60	-3.94	-0.07	-27.05	-11.32	-29.53	-12.20	-2.80	4.59	-17.24	-6.01	4.90	-16.32	-16.14
MaxD	-9.80	1.69	-1.33	1.88	-2.34	0.40	-26.67	-12.03	-4.93	-0.99	-13.46	-2.11	2.13	-7.75	-10.13
MaxD + STP	-5.79	4.91	-2.85	5.19	-0.81	-6.00	-29.34	-7.68	-1.37	1.91	-10.67	-3.25	5.34	-15.75	-8.77
Nsam	-4.51	1.21	1.52	-0.86	-4.99	-1.52	-25.26	-11.19	-1.27	-12.38	-7.87	-6.76	1.77	-4.25	-5.54
Nsam + STP	-0.65	4.36	-0.56	2.48	-3.91	-7.54	-28.12	-6.93	2.49	-9.78	-5.57	**-8.61**	4.97	-14.10	-5.04
Moisture	-9.04	-19.84	-8.16	2.03	-9.61	-1.41	-30.48	-2.64	-11.83	-25.24	-43.77	2.08	1.97	-38.03	-39.89
MoisturePR + STP	-5.06	-15.87	-9.18	5.43	-7.79	-6.88	-32.65	1.67	-8.42	-22.23	-40.78	0.18	5.13	-40.22	-40.04
BD	-1.96	2.02	2.01	2.13	-5.33	2.13	-16.71	0.20	-16.38	1.92	-4.72	2.08	1.92	-8.05	-6.40
BD + STP	1.81	5.20	-0.13	5.50	-5.09	-3.78	-21.96	4.32	-12.31	4.37	-3.09	0.11	5.16	-19.94	-7.10
WaterBD	1.35	-1.82	-1.17	1.17	-0.81	-3.08	-1.66	1.71	-0.57	0.85	-26.92	-0.36	1.98	-0.94	-4.44
WaterBD + STP	5.16	1.52	-3.01	4.53	-0.26	-9.31	-7.47	5.90	3.20	3.32	-25.48	-2.21	5.19	-10.90	-3.42
PR + PR^2 + STP	-20.97	-0.63	-12.88	-1.55	-24.82	-14.38	-27.38	**-18.50**	**-17.16**	1.44	-17.51	-6.87	4.79	-14.16	-19.16
BD + BD^2 + STP	1.71	3.79	1.85	4.99	-4.16	-2.47	-20.16	3.39	-13.73	-2.65	-1.00	0.12	1.85	-21.16	-7.45
Moisture + Moisture^2 +STP	-4.02	-13.77	-6.97	7.66	-6.18	-6.90	-31.63	-3.17	-6.53	-23.25	-56.54	0.63	7.30	-41.76	-40.14
WaterBD+WaterBD^2 +STP	6.77	-0.71	1.45	6.75	1.38	-23.66	-11.39	6.44	5.13	3.04	-23.07	-0.43	7.39	-13.12	0.29

The meaning of the ecological variables can be found in Table 4.2. *Cabe: Carpinus betulus, Capi:Carex pilulifera, Defl: Deschampsia flexuosa, Fehe: Festuca heterophylla,Hehe:Hedera helix,Homo:Holcus mollis Hypu:Hypericum pulchrum Lope:Lonicera periclymenum,Meun:Melica uniflora,Pone: Poa nemoralis,Post: Potentilla sterilis, Qusp: Quercus sp, Rufr: Rubus fruticosus, Tesc: Teucrium scorodonia, Vire: Viola riviniana & reichenbachiana.*

Table A3 Differences in QAICc values between the best models and models related to light for individual species abundance

	Cabe	*Capi*	*Defl*	*Fehe*	*Hehe*	*Homo*	*Hypu*	*Lope*	*Meun*	*Pone*	*Post*	*Qusp*	*Rufr*	*Tesc*	*Vire*
Subplot.location									-16.8				-2.55		**-63.65**
Subplot * STP	**-21.59**		**-21.9**	**-41.71**		**-49.60**	**-97.30**							**-109.70**	
Subplot * G		**-29.52**								**-87.4**	**-252.9**				
PR					**-15.01**			**-8.69**							
Nsam + STP												-3.39			
PR + STP					-13.31										
L	2.19	0.63	1.6	0.88	0.38	1.88	-18.30	1.67	**-32.80**	-12.9	2.06	-3.09	**-7.58**	-20.10	-5.65
L + STP	6.3	0.51	0.96	4.53	2.26	-6.72	-17.60	6.18	-28.40	-8.36	4.15	-3.38	-3.60	-40.10	-3.05
L + L^2 + STP	0.99	-3.89	-8.70	6.15	3.98	-4.39	-39.4	8.41	-27.10	-6.69	0.01	-2.58	-4.52	-38.00	-18.76

The meaning of the ecological variables can be found in Table 4.2. *Cabe: Carpinus betulus, Capi:Carex pilulifera, Defl: Deschampsia flexuosa, Fehe: Festuca heterophylla,Hehe:Hedera helix,Homo:Holcus mollis Hypu:Hypericum pulchrum Lope:Lonicera periclymenum,Meun:Melica uniflora,Pone: Poa nemoralis,Post: Potentilla sterilis, Qusp: Quercus sp, Rufr: Rubus fruticosus, Tesc: Teucrium scorodonia, Vire: Viola riviniana & reichenbachiana.*

Table A4-1 Multiplicative effect of a substantial variation in ecological variables on the abundance of the individual species

Models	Variables	*Cabe*	*Capi*	*Defl*	*Fehe*	*Hehe*	*Homo*	*Hypu*
Subplot* STP	BO-CO, STP50	8.16 [0.39;73.98]		0.03 [0;314329.43]	1.48 [0.02;10.44]		3.99 [0;3698603.72]	0.00 [0.00;1.00]
	TR-CO, STP50	0.82 [0.01;32.46]		0.00 [0;2360506.51]	0.4 [0.01;4.89]		210.28 [0.00;1577505.31]	119.12 [0;2277796.68]
	BE-CO, STP50	5.91 [0.01;50.47]		0.34 [0;3.25]	1.8 [0.12;16.79]		558.7 [0.00;2374051.28]	896.06 [0;23581180.29]
	BO-CO, STP30	0.16 [0;10.53]		0.03 [0;38.51]	0.89 [0.2;10.4]		2.14 [1.00;5.08]	0 [0;3453499.66]
	TR-CO, STP30	0.15 [0;101.2]		0.52 [0.08;14.63]	0.75 [0.13;13.81]		2.11+ [1.15;4.93]	0.51 [0;39875478.2]
	BE-CO, STP30	0.44 [0;32.53]		1.09 [0.08;12.02]	0.66 [0.19;12.62]		1.67 [0.81;4.51]	0.13 [0;4205720.54]
	BO-CO, STP63	1.14 [0.01;11.6]		509.36 [0;1433733.67]	103.55 [0.45;4997944.41]		0.27 [0.02;2084011.1]	3761829.49^{++} [1500931.63;204875274.57]
	TR-CO, STP63	0.1 [0.01;2.34]		143.18 [0;1615470.41]	29.82 [0;1550266.29]		0.02 [0.00;1361095.47]	41402185.49^{++} [7499550.71;235998507.75]
	BE-CO, STP63	0.72 [0.05;9.43]		1522.26 [0;3221966.57]	257.10^{++} [2.83;5118021.62]		1.08 [0.03;49.07]	25781073.34^{++} [3399414.88;181376487.07]
Subplot * G	BO-CO		3.63 [0.13; 3.11E+29]					
	TR-CO		21.00 [0.16; 479781.16]					
	BE-CO		44.82 [0.42; 513645.01]					
	BO.G		1.49 [0.00;4.11]					

	CO.G	0.03 [0.00;36.51]	
	BE.G	2.64 [0.37;638.91]	
	TR.G	1.61 [0.17;205.87]	
PR	PR		0.67 [0.53; 0.85]
PR + STP	PR		0.67 [0.53; 0.85]
	STP30-50		5.99^{++} [2.92;9.37]
	STP50-63		1.42 [0.87;1.94]

Cabe: Carpinus betulus, Capi:Carex pilulifera, Defl: Deschampsia flexuosa, Fehe: Festuca heterophylla,Hehe:Hedera helix,Homo:Holcus mollis Hypu:Hypericum pulchrum.

Table A4-2 Multiplicative effect of a substantial variation in ecological variables on the abundance of the individual species

Models	Variables	*Lope*	*Meun*	*Pone*	*Post*	*Qusp*	*Rufr*	*Tesc*	*Vire*
Subplot.location	BO-CO		0.65 [0.24; 3.46]				9.23^{++} [6.29;19.19]		3.40^{++} [1.52; 27.24]
	TR-CO		2.42 [0.84; 5.16]				1.33 [0.94;1.91]		27.17^{++} [11.13; 62.8]
	BE-CO		2.28 [0.85; 4.61]				1.70 [1.18;2.46]		26.48^{++} [10.53;62.36]
Subplot* STP	BO-CO, STP50							0.29 [0;2199965.86]	
	TR-CO, STP50							0 [0;616579.51]	
	BE-CO, STP50							0.63 [0;518042.58]	
	BO-CO, STP30							1.28 [0;57426880.53]	
	TR-CO, STP30							47.29^{++} [0.2;300.9]	
	BE-CO, STP30							27.69 [0.19;327.09]	
	BO-CO, STP63							27.62 [0;1408914.58]	
	TR-CO, STP63							466.59 [0;13590209.3]	
	BE-CO, STP63							349.99 [0;13083888.5]	
Subplot * G	BO-CO			17.96 [0.06; 88.03]	204.45 [0;764525.14]				
	TR-CO			26.15 [0.24; 180.04]	2402.33 [0;4215.23]				

	BE-CO			45.36 [0.64; 63.05]	869.5 [0.25;1650596.65]	
	BO.G			1.52 [0.06;4.00]	1.51 [0.10;5.52]	
	CO.G			0.02 [0.01;7.55]	0.18 [9.03;2507.85]	
	BE.G			0.51 [0.12;9.69]	1.56 [0.38;85.99]	
	TR.G			0.70 [0.08;7.48]	1.71 [0.17;14.28]	
PR	PR	0.76^{0} [0.66; 0.92]				
Nsam + STP	Nsam					0.60 [0.36; 0.96]
	STP30-50					8.76^{++} [4.39; 12.02]
	STP50-63					1.01^{0} [0.72; 1.39]

Lope:Lonicera periclymenum,Meun:Melica uniflora,Pone: Poa nemoralis,Post: Potentilla sterilis, Qusp: Quercus sp, Rufr: Rubus fruticosus, Tesc: Teucrium scorodonia, Vire: Viola riviniana & reichenbachiana.

Table A5 Multiplicative effect of a substantial variation in ecological variables (in the models related to light) on the individual species abundance

Models	Variables	*Qusp*	*Meun*	*Rufr*
L	L		1.60 [1.04;2.31]	1.18^{0} [1.02;1.36]
L + STP	L	0.89^{0} [0.74;1.02]		
	STP30-50	5.99^{++} [2.92;9.37]		
	STP50-63	1.42 [0.87;1.94]		
$L+L^2+STP$	L at 1st quartile			
	L at median			
	L at 3rd quartile			
	STP30-50			
	STP50-63			

Table A6 Species list and ecological trait

Species	**life form**	**seed bank**	**light**	**soil moisture**
Acer campestre L. subsp. *campestre*	tree		heliophilous	high
Agrostis capillaris L. subsp. *capillaris*	herb	short	heliophilous	
Agrostis stolonifera L. subsp. *stolonifera* var. *stolonifera*	herb		heliophilous	high
Ajuga reptans L.	herb	transient	heliophilous	high
Anemone nemorosa L.	herb	transient		high
Aquilegia vulgaris L. subsp. *vulgaris*	herb	transient	heliophilous	low
Betula pendula Roth	tree		heliophilous	
Brachypodium sylvaticum (Huds.) P.Beauv. subsp. *sylvaticum*	herb		shade	high
Calamagrostis epigejos (L.) Roth subsp. *epigejos*	herb	transient	heliophilous	
Carex divulsa Stokes subsp. *divulsa*	herb		heliophilous	high
Carex flacca Schreb. subsp. *flacca*	herb		heliophilous	high
Carex pallescens L.	herb	short	heliophilous	high
Carex pilulifera L. subsp. *pilulifera*	herb	long	heliophilous	high
Carex sylvatica Huds. subsp. *sylvatica*	herb	short	shade	high
Carpinus betulus L.	tree		shade	
Crataegus laevigata (Poir.) DC. subsp. *laevigata*	shrub		heliophilous	high
Cytisus scoparius (L.) Link subsp. *scoparius*	shrub		heliophilous	low
Dactylis glomerata L. subsp. *glomerata*	herb	transient	heliophilous	high
Deschampsia cespitosa (L.) P.Beauv. subsp. *cespitosa*	herb		heliophilous	high
Deschampsia flexuosa (L.) Trin. subsp. *flexuosa*	herb		heliophilous	
Dryopteris carthusiana (Vill.) H.P.Fuchs	herb		heliophilous	
Dryopteris filix-mas (L.) Schott	herb		shade	high
Epilobium parviflorum Schreb.	herb	short	heliophilous	high
Epilobium tetragonum L. subsp. *tetragonum*	herb		heliophilous	high
Euphorbia amygdaloides L. subsp. *amygdaloides*	herb		shade	high

Fagus sylvatica L. subsp. *sylvatica*	tree		shade	high
Festuca heterophylla Lam.	herb		heliophilous	low
Fragaria vesca L.	herb	short	heliophilous	high
Fraxinus excelsior L. subsp. *excelsior* var. *excelsior*	tree		shade	
Galium aparine L. subsp. *aparine*	herb	transient	heliophilous	
Geranium robertianum L. subsp. *robertianum* écoph. annuel	herb		heliophilous	
Gnaphalium uliginosum L. subsp. *uliginosum*	herb	short	heliophilous	high
Hedera helix L. subsp. *helix*	tree		shade	high
Holcus mollis L. subsp. *mollis*	herb		heliophilous	high
Hyacinthoides non-scripta (L.) Chouard ex Rothm. subsp. *non-scripta*	herb		heliophilous	high
Hypericum androsaemum L.	herb	short		
Hypericum perforatum L. subsp. *perforatum*	herb		heliophilous	low
Hypericum pulchrum L.	herb	short	shade	high
Ilex aquifolium L.	shrub		shade	high
Juncus bufonius L. subsp. *bufonius* var. *bufonius*	herb	short	heliophilous	high
Juncus conglomeratus L. subsp. *conglomeratus* var. *conglomeratus*	herb	short	heliophilous	high
Lamium galeobdolon (L.) L. subsp. *galeobdolon*	herb		shade	high
Lapsana communis L. subsp. *communis*	herb	short	heliophilous	high
Lathyrus linifolius (Reichard) Bässler subsp. *montanus* (Bernh.) Bässler	herb			high
Lonicera periclymenum L. subsp. *periclymenum*	shrub	transient	heliophilous	
Luzula forsteri (Sm.) DC. subsp. *catalaunica* P.Monts.	herb			
Lycopus europaeus L. subsp. *europaeus*	herb	transient	heliophilous	high
Malus sylvestris Mill. subsp. *sylvestris*	shrub		heliophilous	high
Melampyrum pratense L.	herb	transient	heliophilous	high
Melica uniflora Retz.	herb	transient	shade	high
Melittis melissophyllum L. subsp. *melissophyllum*	herb		heliophilous	low
Milium effusum L.	herb	short	shade	high

Moehringia trinervia (L.) Clairv.	herb	short	shade	high
Myosotis arvensis Hill subsp. *arvensis*	herb	short	heliophilous	high
Oxalis corniculata L. var. *corniculata*	herb		heliophilous	low
Pinus sylvestris L.	tree		heliophilous	
Poa annua L. subsp. *annua* var. *annua*	herb	short	heliophilous	high
Poa chaixii Vill.	herb		heliophilous	high
Poa nemoralis L. subsp. *nemoralis* var. *nemoralis*	herb		heliophilous	high
Poa trivialis L. subsp. *trivialis*	herb		heliophilous	high
Polygonatum multiflorum (L.) All.	herb		shade	high
Populus tremula L.	tree		heliophilous	high
Potentilla sterilis (L.) Garcke	herb	short	heliophilous	high
Prunus avium (L.) L. var. *avium*	tree		shade	high
Prunus laurocerasus L.	shrub			
Prunus spinosa L.	shrub		heliophilous	low
Quercus petraea Liebl. subsp. *petraea*	tree		heliophilous	high
Rosa arvensis Huds.	shrub		heliophilous	high
Rubus fruticosus L.	herb	long	heliophilous	high
Ruscus aculeatus L.	herb	transient		
Salix cinerea L.	shrub		shade	high
Scrophularia nodosa L.	herb	short	heliophilous	high
Solanum dulcamara L. var. *dulcamara*	herb	short	heliophilous	high
Solidago virgaurea L. subsp. *virgaurea*	herb		heliophilous	high
Sonchus asper (L.) Hill subsp. *asper*	herb	short	shade	low
Sorbus domestica L.	tree		shade	low
Sorbus torminalis (L.) Crantz	tree		heliophilous	
Stachys officinalis (L.) Trevis. subsp. *officinalis*	herb	short	shade	high
Stachys sylvatica L.	herb	short	heliophilous	high
Stellaria holostea L. var. *holostea*	herb		heliophilous	high
Taraxacum sect. Ruderalia Kischner, H.Øllgaard et Stepanek	herb		heliophilous	low
Teucrium scorodonia L. subsp. *scorodonia*	herb	short	heliophilous	high
Valeriana officinalis L. subsp. *repens* (Host) O.Bolòs & Vigo	herb	transient	heliophilous	high

Veronica chamaedrys L. subsp. *chamaedrys* var. *chamaedrys*	herb	short		
Veronica montana L.	herb	short	shade	high
Veronica officinalis L.	herb	short	heliophilous	low
Vicia tetrasperma (L.) Schreb. subsp. *tetrasperma*	herb		heliophilous	high
Vinca minor L.	herb		shade	high
Viola reichenbachiana Jord. ex Boreau	herb	transient	shade	high

Data source: Julve (2007) for life form, soil moisture and light; Hodgson et al. (1995) for seed bank persistence. The blanks in the table mean information is lacking and the species is not classified.The standard of ecological group classification is in Table 4.1.

Chapter V Discussion

The influence of tree stand attributes or management disturbance on ground flora have been studied in previous studies. Yet, no studies compared the effects of tree stand attributes with disturbance by ground-based logging system, or detected their combined effects on ground flora. Therefore, our study investigated the effects of tree stand attributes and skid trail effects on ground flora at two spatial scales - stand (400 m^2 plot) and fine scale (2.5 m^2 plot). Model comparison method under multiple hypotheses framework (Chamberlin, 1965) was used, to find out the best indicator (or set of indicators) of ground flora diversity. Besides, most studies used *P*-values to distinguish different situations in trends, but the failure to reject the null hypothesis of no trend based on does not test whether the trend is ecologically important. We therefore preferred to use methods that center the analysis around the magnitude or negligibility of effects (Barbier et al., 2009) to estimate the magnitude and direction of each variable on diversity. Finally, for better suggesting the underlying mechanisms (e.g. Ellenberg-based plant groups) or orienting conservation measure (e.g. forest vs non forest plant species), diversity pattern were detected at ecological group level and individual species level.

5.1 Effects of stand attributes and skid trail area on ground flora diversity at stand scale

5.1.1 Best models

In our study tree stand attributes (stand type or basal area) were the best indicators of ground flora diversity even in forest disturbed by ground-based logging system. Stand type was the best indicator of ground flora richness. For abundance, either stand type or basal area of tree species was best, depending on the ecological traits of the ground flora. For example, stand type best indicated the abundance of peri-forest species while the basal area of the main tree species best indicated forest and non-forest species abundance. In a similar vein but with a slightly different species mix, Barbier et al., (2009) found that basal area was a better model in French oak-hornbeam lowland forests than models incorporating tree species richness or evenness at the of 400-m^2 plot scale.

5.1.2 Effects of stand attributes

The standard-with-coppice (SWC) forest can provide a wide variety of environmental conditions (e.g. light, temperature, soil acidity) due to regular harvesting or different rotation cycles among stands; this leads to high species diversity in SWC forests (Ash and Barkham, 1976; Packham et al., 1992). In our study, though the SWC stands in the Montargis forest are no longer regularly cut, they still tend to maintain more species than the mature even-aged stands. This higher ground flora diversity is mainly due to the high richness and abundance of the peri-forest and non-forest successional groups or the intermediate-light species group.

The maturing process from young to mature high forest stands is accompanied by a decrease in ground flora diversity in our study, and this decrease is sharper from pole to mature stage than from sapling to pole stage. Our result was consistent with the meta-analysis by Duguid and Ashton (2013). They demonstrated that diversity in managed even-aged old stands (greater than 50 years of age) in temperate forests significantly decreased compared to even-aged young stands or unmanaged stands. Decreases in species richness in mature stands were also found in the studies by Small and McCarthy (2005) and Olivero and Hix (1998). 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.

Yet, 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. We also found a very heterogeneous response to stand age at the species level: the abundance of two species (*H. Helix* and *E. striatum*) significantly and strongly increased while that of four species (*Q. petraea, I. aquifolium, D. scoparium, Isothecium sp*) sharply decreased. Furthermore, these heterogeneous responses involved species that belonged to the same ecological group. For example, *Q. petraea*, *H. helix* and *I. aquifolium* belong to the intermediate-light group but two of them had a sharp negative response and one of them had a sharp positive response to stand transition from sapling to pole stage.

Our study compared the relative effect of the basal area of oak, beech and hornbeam in an oak-dominant forest. All the successional or light-demanding groups were negatively influenced by the basal area of beech and hornbeam but did not respond to that of oak. The decrease in ground flora diversity with increasing basal area of beech or hornbeam could be related to the “mesification” process (Barbier et al., 2009; Rogers et al., 2008). Namely, in the successional transition phase, the decline in the dominance of oaks in the overstory is accompanied by an increase in abundance of newly established tree species (beech and hornbeam). As a consequence, the stands might experience a considerable turnover in their understory – more precisely, a decrease in herbaceous species richness and abundance – during this process.

5.1.3 Effects of skid trails

When focusing only on the single-variable effects of skid trails, our results were consistent with those of Zenner and Berger (2008) that skid trails promoted the total ground flora diversity at stand scale, forest species diversity was not affected by skid trails, and peri-forest and non-forest species were significantly increased. Besides, the diversity of species with different light-demanding level all increased with increasing skid trail area. However, the incorporation of skid trails as additional effects into our best tree-stand indicators did not lead to a significant improvement in the models’ ability to explain variations in ground flora diversity. This indicates that the effects of skid trails on species richness and abundance vanished when other tree stand indices were already incorporated into the statistical model.

The explanation for this result might be that our sample plots were selected to cover different stand types, not to represent varied skid trail area among plots. As a result, skid trail area varied significantly among stand types in our study (Table 3.1). Due to this correlation, and to the negligible additional effects of skid trails, we can conclude that, in our case, skid trail effects were negligible for the ecological groups that we studied; the single effects detected were in fact due to differences in skid trail area among stand types. 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. Furthermore, 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 trails from these two traits. Finally, as total richness was also unaffected by skid trail area, this means that, on the whole, as many species were positively affected as were negatively affected. Besides, in the results of our investigation at species level, the best models related to tree stand properties (age, stand type or total basal area of oak, beech and hornbeam), with similar results at ecological group level. Furthermore, except for the non-negligible negative response of *Isothecium sp.* and the negligible responses of some species, about 70% of the investigated species (occurrence >25%) showed neither positive/negative nor negligible responses to skid trails. This may be related to a higher level of noise at the species level. Therefore, a higher level of uncertainty for the skid trail effects appeared when we shifted our focus from group level to species level.

5.2 Effects of skid trails, environmental factors and stand attributes on ground flora diversity at fine scale

5.2.1 Best models

The best models for ecological groups included subplot location, soil moisture or soil compaction (PR or BD), depending on which ecological groups (classified by life form, seed bank persistence, light and moisture requirements) the species belonged to and on whether species richness or species abundance was considered. For the majority of ecological groups (8 out of 10 groups), the best indicators of species richness were related to micro-environmental factors (soil moisture or compaction), while the abundance of most groups (7 out of 10) was best indicated by models related to subplot location. The best models for the 15 species we studied were similar – models related to subplot location or its interactive effect with stand type or basal area (12 out of 15 species).

5.2.2 Interaction among ecological factors

For the interaction among ecological variables of disturbance gradient (subplot location), micro-environmental factors (soil moisture, soil compaction, light) and stand type, on the one hand, stands in different rotation stages had significantly different levels of light availability, soil moisture or soil compaction. On the other hand, among the three micro-environmental factors (light, soil moisture and compaction), only one factor - soil compaction - varied among subplot locations in each stand type. This implied that soil compaction was the only factor that was significantly affected by skid trail disturbance, which was consistent with the previous studies that the recovery period of highly compacted soil could last decades.

5.2.3 Effects of skid trails, soil moisture, light and stand type

Subplot location that indirectly represents disturbance gradient was the best indicator for the richness of tree and short-term seed bank species, as well as the abundance of tree species and shade-tolerant species. However, the effects of subplot location depended on stand types: its positive effects compared to controls only occurred in the two older stand types. Stand type as a covariate still played a significantly important role in fine-scale diversity pattern. Skid trails in young stands were denser but narrower than in older stands, and were submitted to fewer and/or less intense disturbances. Indeed, in the two older stand types, we observed wheel ruts produced by machinery as well as soil compaction values on skid trails significantly higher than the paired controls. Furthermore, community stability reflects the ability of resident species to resist change, or, if altered by disturbance, their ability to readjust or recover (Halpern, 1988). By these criteria, the understory plant community in our research area appears to be resilient to the skid trail system. Skid trails did not appear to negatively impact ground flora diversity, on the contrary, it promoted the diversity of some ecological groups (Schumann, et al., 2003).

Soil moisture was the best indicator for the richness of transient seed bank, shade-tolerant, low- and high- humidity species. Sattar Ezzati et al., (2012) got the similar finding that there was no moisture difference between skid trail and undisturbed forest 16-20 years after skidding operations. According to our results, both the richness of low- and high- humidity species were positively affected by soil moisture. The reason could be explained by Qian et al., (1997) that the trend of higher diversity in wetter soil conditions generally agrees with findings that diversity peaks at mesic sites (e.g. Burton et al., 1992; Pausas 1994; Roberts & Gilliam 1995a). Besides, in compacted habitats, soil moisture level may be wetter in spring, fall or winter but drier in summer than average level. This might favor both species with low and high soil wetness preference.

Our study supported the important role of soil compaction only for shrubs (with penetration resistance as the best indicator) and heliophilous species (with bulk density as the best indicator). Higher soil compaction detected on skid trails did not necessarily mean that it will have significant effects on ground flora. One reason may be that the soil compaction level in our study did not reach the level that may affect ground flora. This was supported by Zenner et al., (2007), who found that though traffic intensity had a negative effect on both aspen density and growth, penetration resistance (PR) measured from this traffic was not significantly associated with aspen density and growth. Zenner et al., (2007) explained that the PR values after harvest were below the levels that restrict suckering and growth of aspen. Specific PR values at which root growth is restricted are thought to be between 2,500 and 3,000 kPa for many plant species (Taylor et al., 1966, Greacen and Sands 1980). In our study, the critical value of 2,500 kPa was found only on the wheel tracks (TR) of stands aged of 50 and 63 years. Heninger et al., (2002) used bulk density as soil compaction indicator, and found that reductions in tree height were unrelated to percentage increases in soil bulk density in the 0 to 30cm soil horizon. Higher soil moisture was usually considered to result in more compacted soils (Siegel-Issem et al., 2005; McNabb et al., 2001; Williamson and Neilsen, 2000), and vice versa (Greacen and Sands, 1980; Tan et al., 2005). However, in our study, there was no strong relationship between penetration resistance and moisture (Pearson’s r=0.148, P=0.0898). Besides, the effects of penetration resistance or moisture were only detected at group level but not at species level. More ecological groups were affected by soil moisture compared to soil compaction. Only one study to our knowledge compared the effects of soil moisture and compaction at stand scale, and found that seedling growth rate in the periods 0 - 12 and 12 - 24 months after planting was promoted by higher soil moisture (33%), while penetration resistance had no effect (Hattori et al., 2013).

Light effect compared to control was weak in our study. The study of Zenner et al., (2008) on plot covered with skid trails also failed to detect significant effects of canopy removal intensity on ground flora composition and diversity. Light did not vary among subplot locations in each stand type in our study. In fact, decades after the creation of skid trails, trees nearby are already tall enough so that the canopy cover can be fully developed even with disturbance. This was the case even in the youngest stands (30 years on average), because, although trees were relatively smaller and denser, the skid trails were narrower and the machines used were smaller than in older stands. Buckley et al., (2003) also found that mean canopy cover was just slightly lower on skid trails than in forest.

5.3 General discussion and recommendations for forest management or further research

Networks comprised of road and skid (or tractor) trails are requisite features of forest managed for timber, in which standard equipment such as skidders, forwarders and semi-trailers are used during harvests (Avon et al., 2010, 2013; Buckley et al., 2003). Skid trails were shown to act as conduits and propagated road effects further into forest (Avon et al., 2013). In this study, skid trails at stand scale had the potential of having higher peri-forest, non-forest and light-demanding species (though the responses of these species were rather weak compared the ones to stand attributes). At fine scale, skid trails had higher diversity of tree, short-term seed bank species and shade-tolerant species. This agreed with previous studies that skid trails can be sources for maintaining higher diversity (Trombulak and Frissell, 2000; Gelbard and Belnap, 2003; Milberg and Lamont 1995; Nelson, et al., 2008).

Patches with low disturbance, such as off-skid-trail areas, have been shown to act as species pools, which can provide a source of interior forest species to recolonize the site (Zobel 1997; Berger et al., 2004). However, in research area as in Montargis forest, it is hard to find stands without skid trails. Skid and tractor trails distributed in almost all stand types.

In our research area, mean skid trail area/density was observed to be low compared to other research area. Moreover, though the area of skid trails varied among stand type at different rotation stages, the extremes of highly disturbed stands cannot be found in this forest. Zenner et al., (2007) discussed that sampling has often focused on skid trails that have been subjected to sufficiently high levels of disturbance, so that changes to the soil and vegetation were still visible several years after harvest. Conclusions about skid trail effects studied on these areas may underestimate the areal impact and overemphasize the severity of impact of skidding traffic on stand or landscape scale. Our study confirmed what they suspected. In Montargis forest, the effects of ground-based logging system seems to have been over emphasized if forest management was guided due to studies based on higher disturbance area. However, at fine scale, even under the context of low disturbance in Montargis forest, the role of skid trails is rather important and could not be neglected. Significantly greater soil compaction than control can be detected on or between the wheel track, and high soil compaction positively influenced the diversity of certain species groups.

Our study used four soil compaction indicators: penetration resistance (PR), bulk density (BD), number of local measures to reach 20cm depth (Nsam), maximum depth (Nsam). The results supported our hypothesis that none of the four indicators was definitely more appropriate than the others for indicating ground flora diversity. For the ecological groups that had best models related to soil compaction indices, their compaction indicators varied among these four indicators: the best indicator of the richness of shrub, herb and heliophilous species and the abundance of oak species were MaxD, PR, BD and Nsam respectively (though the effects of MaxD and Nsam turned out to be negligible). In review of the previous studies, it has been shown that PR measurement is tenfold more sensitive to soil compaction variation than BD sampling (Vazquez et al., 1991). According to our results, PR is the most sensitive since greater PR can be detected on skid trails than on controls in the two older aged stands (STP50 and STP63), the second were BD and Nsam of which greater value were found on skid trails only in the oldest stand (STP63). The least sensitive one is MaxD which did not show difference between locations on and off skid trails. Nsam has never been used in previous studies. We thought it was useful indicator especially in forests with relatively higher stone content. We hypothesized that when soil is compacted, relatively denser aggregation of small stones in the same soil volume might happen, so that Nsam increased. Finally, applying the same set of the four compaction indicators into other research area would help us to better describe or compare the compaction status than measuring only PR or BD as in previous studies.

At fine scale, our sampling design lacks the forests with very late stages of high forest rotation. Further investigation on the skid trail effects in older stands is still needed. This is because, 1) we have detected an increasing trend of soil compaction with stand age, much higher levels of soil compaction and its impact on ground flora might be found during the maturing process of these stands; 2) on the other hand, light, soil moisture and compaction were detected to varied among stand types, the relative role of these micro-environmental factors could be different in more mature stands; 3) Concerning scale effects, the stand types of fine-scale study were more restricted to younger stands than the stand types studied at stand scale, which is one of the reasons impedes our comprehensive understanding of scaling effects of skid trails.

Many studies have proved that the soil nutrient may be affected by soil compaction, and in turn affect ground flora diversity, thus soil nutrient on skid trails on its effects on plant could also be studied.

Pickett (1980) noted that the persistence of certain species in plant communities requires disturbance. In particular, disturbances can significantly enhance ecological heterogeneity at multiple scales (White and Jentsch 2001; Schoennagel et al., 2008; Mori and Lertzman 2011). However, there is growing concern that timber harvesting may have deleterious effects on the long-term maintenance of species diversity and composition (Burton et al., 1992), particularly with increasing disturbance intensity (e.g., clearcut). In the coming years, French silviculture is likely to dramatically change in relation to global warming and biomass fuel needs: shortening of cycles, increased timber harvesting and more frequent penetration of logging vehicles (Avon et al., 2013). Therefore, longer-term study of skid trail effects would be needed to validate the main findings of our study.

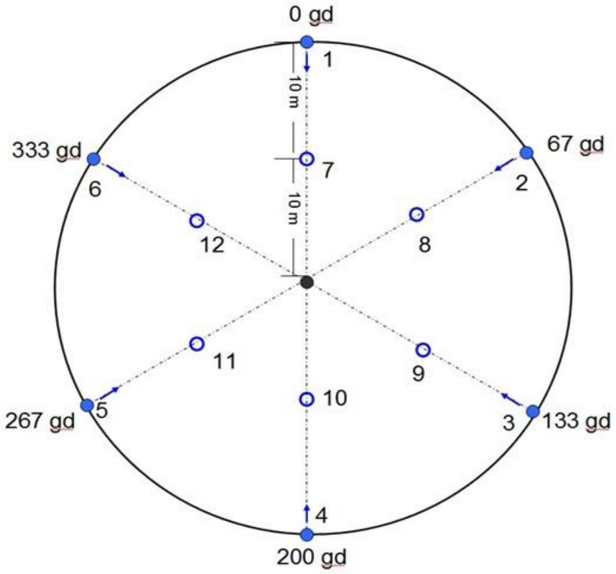
5.4 Field study and analyses in progress

5.4.1 Tractor trail effects (field work and data analysis has already been finished)

The research objective was to compare the effects of old and recent tractor trails on ground flora, as well as to find out the dominant factor among subplot location, soil moisture, soil compaction and light. Old tractor trails were marked in 2000 that within or cross the 400 m^2 plots; recent tractor trails were those found established since 2000. Unlike skid trails, tractor trails are short in length and not straight. They and have no regular distribution in the forest. Tractor trails potentially occur anywhere, usually used for hauling out the cut wood from interior forest. In 2011, we selected 54 stands belonging to four stand types, including one even-aged high stand and three conversion stands from previous standard-with-coppice: 1) HF100: 100 years old high stand; 2) SWC1: coppice-with-standards converted to irregular stand; 3) SWC2: coppice-with-standards converted to medium-diameter regular stand; 4) SWC3: coppice-with-standards converted to large-diameter regular stand. Some plots only had either old or new tractor trails, while some plots had both. In total, there were 56 old tractor trails and 54 recent tractor trails. Two 0.5m-×-5m subplots were set on each tractor trail: on the wheel track of tractor trail (TR) and between the two wheel tracks of tractor trail (BE). We also set a 0.5m-×-5m control subplot in the plot where there was no tractor trail and had the similar canopy cover as (visually) similar as possible as the tractor trails. We set up a 22m-radius circular plot from the center of the quadrats for dendrometry, measuring diameter at breast height (“DBH”, in cm) for each tree. We made vegetation investigation and measured penetration resistance (PR), bulk density (BD) and light on four 0.5m-×-5m subplots systematically set in each 400m_2 quadrat.

5.4.2 GNB projects (field work finished)

The research questions were: 1) What is the response of ground flora to soil compaction and stand attribute in managed and unmanaged forests (1000 m^2)? 2) What is the response of the ground flora to soil compaction gradient? 3) What are the effects of skid and tractor trails on ground flora? There are 50 plots (1000 m^2) in total which located in four national forests (Haut-Tuileau, Rambouillet, Verrières, Parroy), half are managed stands and half unmanaged. We did soil sampling for both 1000 m^2 plot and 2.5 m^2 subplots, and made vegetation investigation for 2.5 m^2 subplots (vegetation investigation in 1000 m^2 plot have already been done by other colleagues since 2010). Soil compaction was measured by penetrologger. The soil compaction measurement follows the same protocol as in Montargis forest. The only difference is the number and location of sampling in each plot. There are 12 measures of PR measures in 1000 m^2 plot, and the locations are shown in Fig 5.1. The method of setting 2.5 m^2 subplots were as follows (Fig 5.2): 1) In managed forest, we set 3 systematic subplots. If there were skid or tractor trail, we set a subplot on the wheel track of each skid trail, as well as a control subplot in undisturbed area. If there was more than one tractor or skid trail, we chose the closest to the middle point of 1000 m^2; 2) In unmanaged forest, we set 3 systematic subplots as in managed forest. The soil compaction sampling in subplots was the same as in Montargis forest.



Penetrations 7 to 12 are the middle points of the subplots, so we don't sample them here but in subplots.

Figure 5.1 soil compaction sampling in 1000 m^2 plot (The arrows represent the directions of new penetration sampling when meet stones)

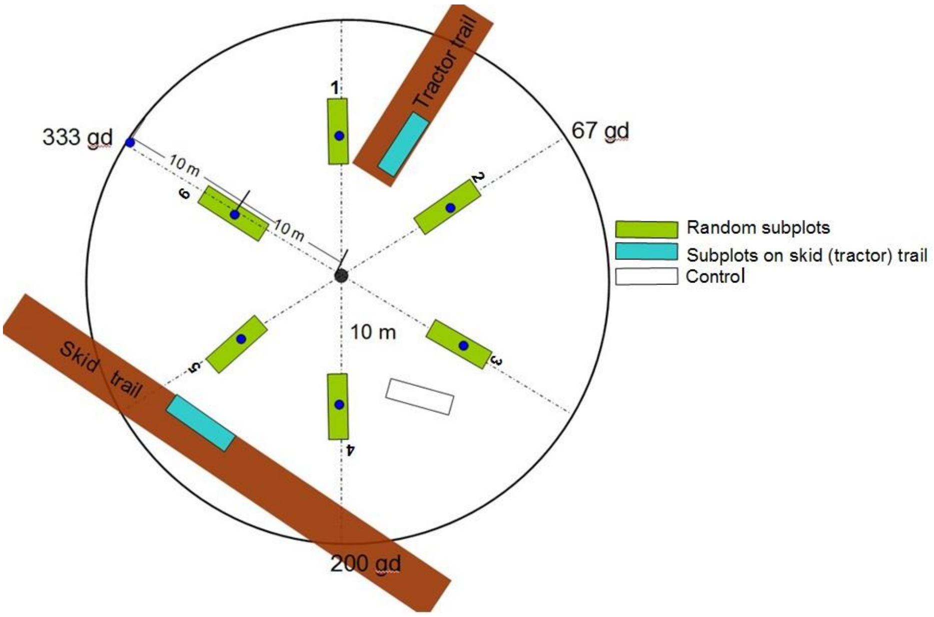


Fig 5.2 subplots setting (2.5 m^2) in 1000 m^2 plot

Chapter VI Conclusion

In this thesis, the effects of stand attributes and skid trails on ground flora diversity at stand scale (400 m^2 plot) and fine scale (2.5 m^2 plot) were studied in Montargis forest in the northern half of France. Model comparison method under multiple hypotheses framework was used, to find out the best indicator (or set of indicators) of ground flora diversity. Besides, methods that center the analysis around the magnitude or negligibility of effects (Barbier et al., 2009) were used to estimate the magnitude and direction of each variable on diversity. Finally, for better suggesting the underlying mechanisms (e.g. Ellenberg-based plant groups) or orienting conservation measure (e.g. forest vs non forest plant species), diversity pattern were analyzed at ecological group level and individual species level.

At stand scale, we studied the individual and combined effects of tree stand attributes (age, stand type, basal area) and skid trail area on ground flora diversity. We selected 96 oak-dominated stands including even-aged high-forest (29, 55 or 104 years old) and standard-with-coppice stands. The results lead to the conclusion that tree stand attributes (stand type or basal area) were the best indicators of ground flora diversity even in forest disturbed by ground-based logging system. At ecological group level, among-plot floristic variations were mostly associated to stand type or tree species basal area, depending on the successional traits or light preference of the species group. Although we found significant effects of skid trail area on ground flora except for forest species, the effects of skid trail area disappeared when tree stand attribute effects were incorporated into the statistical model. At species level, only *Fissidens sp.* had a non-negligible response to skid trails, while the responses of some species were uncertain. In the Montargis forest under current levels of mechanical harvesting, the stand-scale effect of skid trails on the richness and abundance of ecological groups is very likely weak compared to the influence of tree stand attributes. Yet, more uncertainty remained at individual species abundance level. Considering that mechanical harvesting is becoming more commonly used in forest management, the situation may change; we should expect stronger effects in the long-term, especially if skid trails area increase or if skid trails were more compacted.

At fine scale, we investigated understory diversity pattern in three high forest types of varying tree maturity with skid trail system. We compared the effects of subplot location, micro-enviromental factors (soil moisture, soil compaction, light) and stand attribute (stand type, basal area)on ground flora. We selected 36 oak even-aged stands of 30, 50 and 63 years old. Sampling subplots were placed in four locations in each plot: skid trail centre, wheel track, skid trail edge plus an off-trail control plot inside the forest. Results showed that soil compaction, soil moisture and light significantly varied among stand types. Soil compaction was the only factor that was affected by skid trail disturbance: Higher soil compaction was detected on the track of skid trails in the 50 and 60 years old stands, while soil moisture and light did not vary with subplot location in each stand type. At species group level, the best models included subplot location, soil moisture or soil compaction (PR or BD), depending on which ecological groups (classified by life form, seed bank persistence, light and moisture requirements) the species belonged to and on whether species richness or species abundance was considered. Stand type as a covariate played a significantly important role in fine-scale diversity pattern. At species level, subplot location was the only factor that showed non-negligible effects on species abundance. Disturbance indirectly represented by subplot locations can override the environmental factors and become the best indicator. Higher species abundance on skid trails occurred in the 30- and 63-year-old stands. In our study, skid trails had either no impact or a positive impact on ground flora diversity. We indeed found no negative effects of skid trails on flora diversity. However, in our research area, mechanized harvesting is relatively recent and harvesting practices with heavier machines is still likely to happen. Furthermore, our study was conducted only in young stages of the forestry cycle (< 63 yr), further investigation on the skid trail effects in older stands is still needed. This is because, on the one hand, we have detected an increasing trend of soil compaction with stand age, much higher levels of soil compaction and its impact on ground flora might be found during the maturing process of these stands; on the other hand, light, soil moisture and compaction were detected to be vary among stand types, the relative role of these micro-environmtal factors could be different in the older stands.

Our sampling design at fine scale lacks the forests with very late stages of forest rotation. Further investigation on the skid trail effects in older stands is still needed. Many studies have proved that the soil nutrient may be affected by soil compaction, and in turn affect ground flora diversity, thus soil nutrient on skid trails on its effects on plant could also be detected. French silviculture is likely to change in terms of shortening of cycles, increased timber harvesting and more frequent penetration of logging vehicles (Avon et al., 2013). Therefore, longer-term study of skid trail effects would be needed to validate the main findings of this thesis.

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Liping WEI

Impacts des caractéristiques du peuplement et des cloisonnements sur la biodiversité floristique en forêt de plaine

Résumé :

Le maintien ou l'amélioration de la biodiversité est un des objectifs importants de la gestion forestière durable. La flore du sous-bois, qui représente la partie la plus diversifiée de la flore dans les forêts tempérées, joue des rôles écologiques importants. Pourtant, elle pourrait être impactée par l'augmentation de la mécanisation de la gestion forestière. A l'échelle de la parcelle, nous avons étudié en forêt de Montargis les effets simples et combinés de caractéristiques du peuplement et de la surface en cloisonnement sur la diversité floristique du sous-bois (richesse et abondance). Les caractéristiques du peuplement (type de peuplement ou surface terrière des essencesà étaient les meilleurs indicateurs de la diversité du sous-bois. La surface des cloisonnements avait un effet négligeable. A plus petite échelle – à l'intérieur du cloisonnement – nous avons étudié la réponse statistique de la diversité du sous-bois à la position dans ou hors du cloisonnement, à des facteurs micro-environnementaux (humidité du sol, compaction du sol, lumière) et aux caractéristiques du peuplement. A cette échelle, les meilleurs modèles incluaient pour les groupes écologiques la position par rapport au cloisonnement, l'humidité du sol et/ou la compaction du sol, selon le groupe écologique considéré. Au niveau espèce, la position par rapport au cloisonnement était le facteur dominant. Globalement, les cloisonnements avaient soit pas d'effet soit un impact positif sur la diversité floristique de sous-bois. Ces résultats ont dépendants du contexte écologique et historique de la forêt de Montargis. L'utilisation d'engins plus lourds ou des passages répétés sur une plus longue période pourraient changer ces conclusions.

Mots clés : Groupe écologique; Type de peuplement; Surface terrière; Compaction du sol; Humidité du sol; Comparaison de modèles; Cloisonnement d'exploitation; Perturbation

Effects of stand attributes and skid trails on ground flora diversity in lowland forests

Summary:

Maintaining or improving biodiversity is an important goal of sustainable forest management.Ground flora, which is responsible for most floristic diversity in temperate forests, plays multiple important roles in biodiversity but may be impacted by the increasing mechanisation of forest practices. At stand scale, we investigated in Montargis forest the individual and combined effects of tree stand attributes and skid trail area on ground flora diversity. Tree stand attributes (stand type or basal area) were the best indicators of ground flora diversity, depending on the successional traits or light preference of the species group. The effects of skid trail area were negligible. At finer scale, we studied plant response to skid trail disturbance (represented by subplot on and off skid trails), micro-environmental factors (soil moisture, soil compaction, light) and stand attribute (stand type, basal area). The best models for ecological groups included subplot location, soil moisture or soil compaction, depending on which ecological groups (classified by life form, seed bank persistence, light and moisture requirements) the species belonged to. Stand type as a covariate played a significantly important role in fine-scale diversity pattern. Subplot location was the dominant factor at species level. In conclusion, skid trails had either no impact or a positive impact on ground flora diversity. These results are dependent on the context of Montargis forest (ecological and historical), especially that mechanized harvesting is relatively recent. The employment of heavier machines and increased number of passages is likely to happen. This might induce greater soil compaction and negative effects on plant.

Keywords : Ecological Group; Stand Type; Basal Area; Soil Compaction; Soil Moisture; Model Comparison; Equivalence Tests; Disturbance

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