Review

Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests

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Abstract

Tree species composition is a primary attribute of forest ecosystems, and is often manipulated by silvicultural practices. Forest management to diversify tree species is now being promoted to favor biodiversity. To assess the soundness of this policy we reviewed and analyzed the literature on the relationship between tree species composition and floristic diversity, including the mechanisms involved therein. Coniferous forests generally provide less diversified vascular understories than broadleaved forests. At the tree species scale, there are not enough reports to draw firm conclusions on the effect of any particular species. Mixing of deciduous and coniferous tree species generally affects understory diversity, but in almost all cases maximum diversity is observed in one of the pure stands, not in mixed stands. Understory vegetation is influenced by overstory composition and structure through modifications of resource availability (light, water and soil nutrients) and other effects, such as physical characteristics of the litter layer. Overstory light transmittance and diverse properties of forest litter are factors that have been most fully studied to date, but other factors such as throughfall water quantity and chemistry may also play a role. While the relative importance of mechanisms that account for the effect of overstory on understory biodiversity has often been discussed, these mechanisms have rarely been the subject of formal experiments. Overall, varying management practices and site attributes make it difficult to generalize results. They combine with the effects of tree species in influencing understory vegetation diversity, but they have been rarely considered. Future research is needed to gain a better understanding of the relationship between overstory and understory diversity and establish general laws.
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Keywords: Forest; Biodiversity; Tree species; Understory vegetation; Light; Litter; Water flows

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1. Introduction

In managed forests, which cover most temperate forests and an increasing proportion of the boreal forests, the choice of tree species is one of the forester's fundamental acts. Owing to the dominant position of trees in forests and their impact on various ecological gradients, the identity and composition of tree species can be expected to influence plant biodiversity, *i.e.* understory vegetation diversity and composition (Bratton, 1976; Palik and Engstrom, 1999). As a direct consequence, tree species composition and diversity is considered as a biodiversity indicator (MCPFE, 2003). Many assumptions are often made, *e.g.*, that hardwoods are more favorable to biodiversity than conifers, or that mixed stands are more favorable than pure ones. However, these assumptions may not always be sound. Moreover, the mechanisms involved in the effects of tree species on vegetation are not yet fully understood. Policy makers and researchers need information about how tree species impact on understory vegetation diversity. Mitchell and Kirby (1989) reviewed results chiefly for British forests, and Hart and Chen (2006) have briefly discussed overstory composition effects on understory vegetation. Here we take this assessment further by (i) reviewing studies on the effects of tree species or diversity on understory vegetation in all boreal and temperate forests (mountain forests included), and (ii) examining many of the mechanisms involved (except for physiological characteristics of tree species). In the first part, we review work concerning the global relationship between tree species and understory vegetation diversity. Most of the work does not report on management practices and we therefore do not consider these in this first part, although they can greatly affect understory vegetation. In the second part, ecological mechanisms potentially involved in the overstory–understory relation are reviewed. We mainly consider light, water, nutrients, physical effects of litter and phytotoxic compounds. Each factor is dealt with as follows: (i) a brief general introduction to the factor, (ii) how tree species affect this factor, and (iii) the responses of understory diversity and (or) composition to changes in this factor among tree species. In the third part, we focus on the potential interaction between management practices and (or) site characteristics and tree species in their influence on understory diversity. We then give some perspectives to improve the study of the effects of tree species on understory vegetation diversity; we especially stress the importance of analyzing different ecological groups, particularly those related to potential ecological mechanisms.

2. Methods

Papers were selected on two online bibliographic databases: ISI Web of Knowledge and Science Direct Navigator, over all the available years. We used ten requests, containing six or seven key words each (requests are available from the authors). We selected about 700 potentially interesting articles. We reviewed the reference lists of about 200 of these, and for about 50 of them a search for other papers citing them was made.

We take "overstory species" to mean woody species of the tree strata, excluding climber species, and "understory species" bryophytes, herbaceous and woody species growing on the forest floor (generally less than 2 m high). Epiphytic vegetation was not taken into account. We often differentiate "conifers" from "hardwoods", which is a common classification of tree species. Conifers are tree species with needles (mostly persistent, but not always, *e.g. Larix* sp.), and hardwoods are tree species with leaves (mostly deciduous, except for some species such as *Quercus ilex*). A "plantation" is a forest with trees deliberately planted, while in a "naturally regenerated forest" trees have grown from seeds naturally present in the soil. An "old forest" is a forest with a continuous sequence of tree generations, the number of which ranges among studies.

Biodiversity descriptors are noted as follows: SR = specific richness (number of species), H' = Shannon diversity index (Margalef, 1958), and E = equitability. E is defined as $H'/H'\max$ with $H'\max = \ln(\mathrm{SR})$ by one of the two authors cited who used this descriptor (Augusto et al., 2003), but it is not defined by the other one (Nagaike, 2002). We note that E defined thus is not the best quantifier of species equitability (Gosselin, 2006).

More than half of the analyzed data gave only mean values, without variability information. It was therefore not possible to carry out a classical meta-analysis. Instead, we performed a binomial test (with software R Version 2.4.1). Thus we tested whether the ratio of vascular SR under hardwoods to vascular SR under conifers was greater than 1 by estimating the one-tailed probability of observed data under the null model of a 0.5 probability that vascular SR (hardwoods)/vascular SR (conifers) was greater than 1 (data from Table 1). SR of bryophytes

Table 1

Understory vegetation diversity variations between hardwood and coniferous dominant tree species ("Difference Har.-Con.": sign of the difference between understory descriptor for hardwood species and understory descriptor for coniferous species); mean values in italics are approximate (read on figures); statistical tests were performed by authors on the difference Har.-Con., except Augusto et al. (2003) who tested the ratio Har./Con.)

Reference	Hardwood dominant species	Coniferous dominant species	Understory descriptor	Difference Har.-Con.	Significance	Mean values (±S.D.)
Daubenmire (1930)	*Fagus* sp.-*Acer* sp. association	*Tsuga canadensis* association	Herbaceous SR	+	?	14–1
			Shrubs SR	+	?	4–0
Auclair and Goff (1971)	*Acer saccharum, Quercus alba, Q. rubra, Q. velutina, Tilia americana*	*Abies balsamea, Picea glauca, Pinus banksiana, P. resinosa, P. strobus, Thuja occidentalis, Tsuga canadensis*	Herbaceous SR	+	?	*51.0 (±3.7) − 36.9 (±6.2)*
			Shrubs SR	+	?	*11.7 (±3.1) − 10.4 (±2.8)*
Beatty (1984)	*Acer saccharum* and *Fagus grandifolia*	*Tsuga canadensis* codominant with *Acer saccharum* and *Fagus grandifolia*	Vascular SR	+	?	19 − 13
Teuscher (1985)	*Fagus sylvatica*	*Picea* sp.	Herbaceous SR	+	?	?
Amezaga and Onaindia (1997)	*Quercus robur* (mixed with *Fagus sylvatica, Fraxinus excelsior* and *Castanea sativa*)	*Pinus radiata*	Vascular SR	+	**	33.3 (±1.07) − 22.5 (±0.83)
		Larix kaempferi	Vascular SR	+	*	33.3 (±1.07) − 22.7 (±10.97)
Saetre et al. (1997)	*Betula* sp. (*B. pendula* and *B. pubescens*) mixed with young *Picea abies*	*Picea abies*	Vascular SR	−	ns	7.44 − 8.80
			Bryophytes SR	−	ns	9.12 − 10.30
Skov (1997)	*Fagus sylvatica*	*Picea abies, P. sitchensis, Abies grandis, A. nordmanniana, Thuja plicata, Pseudotsuga menziesii…*	Vascular SR	+	?	14.29 − 11.27
	Quercus robur		Vascular SR	+	?	17.81 − 11.27
Emmer et al. (1998)	*Fagus sylvatica* (>50%)	*Picea abies*	Vascular + trees SR	+	?	12.9 (±5.3) − 8.1 (±4.6)
			Vascular + trees *H'*	+	?	1.75 (±0.42) − 1.19 (±0.51)
Fahy and Gormally (1998)	*Quercus petraea* (or its hybrid with *Q. robur*)	*Picea sitchensis*	Vascular + bryophytes SR	+	?	17 (±2.11) − 5.6 (±1.96)
Brosofske et al. (2001)	*Quercus rubra, Populus grandidentata, Acer rubrum, Betula papyrifera*	*Pinus resinosa*	Vascular + bryophytes SR	−	ns	25.9 − 26.6
		Pinus banksiana	Vascular + bryophytes SR	−	ns	25.9 − 31.1
		Pinus resinosa	Vascular + bryophytes *H'*	+	?	1.80 − 1.68
		Pinus banksiana	Vascular + bryophytes *H'*	−	?	1.80 − 1.95
Reich et al. (2001)	*Populus tremuloides*	*Pinus banksiana*	Vascular SR	+	?	*51.1 − 44.7*
	Populus tremuloides	*Pinus banksiana*	Bryophytes SR	+	?	*32.2 − 24.8*
	Populus tremuloides	*Picea mariana*	Vascular SR	+	?	*51.1 − 17.0*
	Populus tremuloides	*Picea mariana*	Bryophytes SR	+	?	*32.2 − 28.2*
Nagaike (2002)	*Quercus crispula*	*Larix kaempferi*	Vascular SR	−	*	35.7 (±9.6) − 48.1 (±16.1)
	Quercus crispula	*Larix kaempferi*	Vascular *H'*	−	ns	4.09 (±0.60) − 4.60 (±1.02)
	Quercus crispula	*Larix kaempferi*	Vascular E	−	ns	0.80 (±0.06) − 0.83 (±0.09)
Qian et al. (2003)	*Populus tremuloides*	*Picea mariana*	Herbaceous SR	+	?	14.2 − 10.0
	Populus tremuloides	*Picea mariana*	Woody SR	+	?	6.3 − 5.2
Augusto et al. (2003)	*Fagus sylvatica*	*Abies alba*	Vascular + bryophytes + trees SR	−	**	?
	Fagus sylvatica	*Abies alba*	Vascular + bryophytes + trees *H'*	−	**	?
	Fagus sylvatica	*Pseudotsuga menziesii*	Vascular + bryophytes + trees *H'*	−	*	?
Nagaike et al. (2005)	*Fagus crenata*	*Cryptomeria japonica*	Vascular SR	−	?	45.2 − 65.4
	Quercus crispula and *Q. serrata*	*Cryptomeria japonica*	Vascular SR	−	?	47.3 − 65.4

Table 2
Understory vegetation diversity variations among hardwoods and among coniferous dominant tree species ("Difference Sp1–Sp2": difference between understory descriptor for species 1 and understory descriptor for species 2; mean values in italics are approximate (read on figures); statistical tests were performed by authors on the difference Sp1–Sp2, except for Augusto et al. (2003) who tested the ratio Sp1/Sp2)

Reference	Dominant tree species 1	Dominant tree species 2	Understory descriptor	Difference Sp1–Sp2	Significance	Mean values (±S.D.)
Hardwood species						
Brunet et al. (1996)	*Fagus sylvatica*	*Quercus robur* (or *Q. petraea* in a few cases), sometimes codominant with *Carpinus betulus*	All vascular SR	−	?	13.54 − 24.95
			Forest herbaceous SR	0	?	6.95 − 6.95
			Other herbaceous SR	−	?	4.26 − 10.53
			Woody SR	−	?	2.34 − 7.47
Skov (1997)	*Fagus sylvatica*	*Quercus robur*	Vascular SR	−	?	14.29 − 17.81
Nagaike et al. (2005)	*Fagus crenata*	*Quercus crispula* and *Q. serrata*	Vascular SR	−	?	45.2 − 47.3
Coniferous species						
Hill (1979)	*Picea abies*	*Pinus* sp.	Vascular *H′*	−	?	?
	Picea abies	*Pinus* sp.	Bryophytes *H′*	0	?	?
	Picea abies	*Larix* sp.	Vascular *H′*	−	?	?
Økland and Eilertsen (1996)	*Picea abies*	*Pinus sylvestris*	Vascular SR	+	?	10.8 − 5.1
	Picea abies	*Pinus sylvestris*	Bryophytes + lichens SR	+	?	12.3 − 10.4
Amezaga and Onaindia (1997)	*Pinus radiata*	*Larix kaempferi*	Vascular SR	−	ns	22.5 (± 0.83) − 22.7 (± 10.97)
Hedman et al. (2000)	*Pinus palustris*	*Pinus taeda*	Herbaceous SR	+	*	14.69 − 11.68
	Pinus palustris	*Pinus elliottii*	Herbaceous SR	+	*	14.69 − 12.70
	Pinus taeda	*Pinus elliottii*	Herbaceous SR	−	ns	11.68 − 12.70
	Pinus palustris	*Pinus taeda*	Woody SR	+	ns	7.41 − 6.39
	Pinus palustris	*Pinus elliottii*	Woody SR	−	ns	7.41 − 8.38
	Pinus taeda	*Pinus elliottii*	Woody SR	−	*	6.39 − 8.38
Brosofske et al. (2001)	*Pinus resinosa*	*Pinus banksiana*	Vascular + bryophytes SR	+	ns	31.1 − 26.6
	Pinus resinosa	*Pinus banksiana*	Vascular + bryophytes *H′*	+	?	1.95 − 1.68
Reich et al. (2001)	*Picea mariana*	*Pinus banksiana*	Vascular SR	−	?	*17.0 − 44.7*
	Piceamariana	*Pinus banksiana*	Bryophytes SR	+	?	*28.2 − 24.8*
Augusto et al. (2003)	*Picea abies*	*Pseudotsuga menziesii*	Vascular + bryophytes + trees *E*	−	*	?
	Picea abies	*Pinus sylvestris*	Vascular + bryophytes + trees *E*	+	*	?

and shrub species were not well enough documented to be tested. The same was the case for other descriptors based on *H′* or *E*. It would have been interesting to make an internal comparision of tree species (instead of grouping hardwood species and conifer species), but here again data were too sparse for such analysis (Tables 1 and 2).

3. Response of understory vegetation diversity to overstory

The effect of tree species diversity on understory vegetation can be studied (i) by the effect of the dominant tree species (which occupied more than 70–80% of total cover or basal area) and (ii) by the effect of tree species richness, mixing degree or global composition. We deal with both approaches below.

3.1. Differences in understory diversity influenced by dominant tree species

It is generally considered that conifers are less favorable to understory diversity than deciduous trees. In the published data

(Table 1) for understory vascular SR there were 10 results with higher SR under hardwoods and four results with higher SR under conifers. Thus the ratio of understory vascular SR (hardwoods) to understory vascular SR (conifers) was significantly higher than 1 ($p = 0.029$). These ratios and those for other understory groups are plotted in Fig. 1. As we see, values greater than 1 were mostly less than 2: SR is thus often higher under hardwoods, but is rarely doubled. We note that bryophyte diversity has very seldom been investigated.

Fewer studies compared hardwood (or coniferous) species internally (Table 2). No statistically significant trend appeared at the species level as data was insufficient. Among hardwoods, three studies compared *Fagus* sp. and *Quercus* sp., and all reported a higher vascular SR in *Quercus* sp. stands. Among conifers, three studies compared *Picea* sp. and *Pinus* sp. The results were conflicting: vascular diversity was higher under *Pinus* sp. in two studies (and lower in the third), while bryophyte diversity was higher under *Picea* sp. in two studies (and no different from under *Pinus* sp. in the third). On the whole, coniferous species from the *Pinus* and *Larix* genera appeared to promote a diversified understory (Tables 1 and 2).
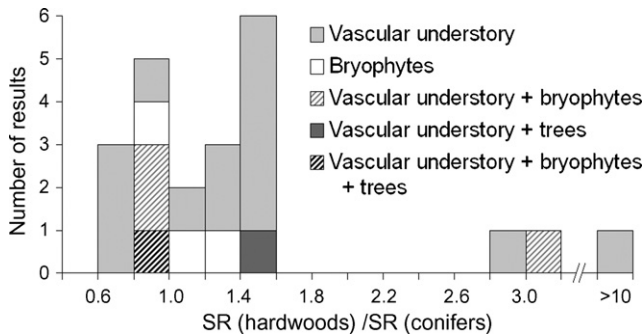
Fig. 1. Distribution of the ratio of species richness under hardwoods to species richness under conifers.

In all cases, most existing studies suffer from a lack of statistical testing to evaluate the significance of the differences stated, and (or) from a lack of standard deviation values, which would have enabled us to carry out a useful meta-analysis.

3.2. Understory diversity response to mixed tree species

By increasing resource diversity, mixed stands have been assumed to host a more heterogeneous and species-rich flora than pure stands (Hill, 1992). However, the superiority of two-species mixed stands over pure stands has rarely been proved; only Jobidon et al. (2004) explored a quadratic relation between understory diversity and mixing degree, and found that a nearly equal mixture of *Picea mariana* and hardwoods was most favorable to SR and *H′* of herbaceous plants (Table 3). Other authors explored only linear relations, but only half of them justified this choice.

Mixing degree has been studied mainly in mixed deciduous–coniferous stands (Table 3). Of the 12 studies of vascular diversity (SR or *H′*), nine reported an effect – positive or negative – of mixing degree on vascular diversity. For the authors who studied linear relations, the sign of the effect depended on the tree species: in *Fagus sylvatica–Picea abies* stands, the relative abundance of *P. abies* had a positive effect on bryophyte SR or *H′* (Lücke and Schmidt, 1997 and Ewald, 2000, respectively), and no systematic effect on herbaceous SR or *H′*; in *Acer saccharum* (and other hardwoods)–*Tsuga canadensis* stands, the relative abundance of *T. canadensis* had a negative effect on herbaceous *H′* in two studies (Lewin, 1973; Hicks, 1980), and its absolute abundance had no effect on herbaceous SR in one study (Williams et al., 1999).

It is important to distinguish canopy and sub-canopy tree species. The development of the latter generally had a negative effect on herbaceous SR, as observed for *Carpinus betulus* (Kwiatkowska, 1994), *Prunus serotina* (Godefroid et al., 2005), *Rhododendron maximum* (Baker and Van Lear, 1998) and *Leucothoe recurva* (Hicks, 1980).

Six studies investigated the effects of tree diversity on understory. Three authors studied tree *H′* effect on vascular diversity. All found a positive effect on vascular SR (Helliwell, 1978), herb *H′* (Hicks, 1980) or "herb accumulation rate" (Lenière and Houle, 2006), which is defined as the parameter "*a*" of the regression herb SR = *a** sampling area. Helliwell

(1978) observed this positive correlation only for "ordinary forests", which excluded old forests and plantations (in these two last types effects were not significant). Auclair and Goff (1971) plotted tree SR and herb SR, and found a positive relation between them. However, they considered all successional stages: apparently this positive relation may not be valid when considering each successional stage individually (pioneer, successional, climax). For bryophytes SR, Pharo et al. (2000) showed a positive relation with tree SR in hardwood Australian forests, while this correlation was not significant in planted or semi-natural British forests (Humphrey et al., 2002).

Finally, multivariate methods revealed specific features in understory species composition as a function of (i) dominant tree species (Légaré et al., 2001), (ii) opposition between pure and mixed stands (Saetre et al., 1997), or (iii) global tree species composition (Gilliam et al., 1995; Humphrey et al., 2002 for bryophytes; Thomsen et al., 2005). These results are difficult to summarize due to the idiosyncratic nature of each set of factorial axes.

4. Ecological mechanisms of tree species effects

Some of the studies cited above showed variations in understory diversity and (or) composition in relation to tree species. However, these results are correlative and so cannot establish causality; they would have had more weight if the mechanisms accounting for the relations between overstory identity and understory diversity had been identified (Palik and Engstrom, 1999).

4.1. Changes in resource availability

4.1.1. Understory light
Light is commonly considered to be the major limiting factor of forest vegetation cover and (or) richness (Hill, 1979; Kirby, 1988; Bazzaz, 1990; Jennings et al., 1999). Understory light is closely dependent on the canopy structure. Air temperature and air humidity in the understory are also dependent on canopy structure, particularly canopy density (Sharpe et al., 1996). Variations of these factors among tree species have been observed (Hunter, 1990; Porté et al., 2004) and are sometimes discussed as affecting understory flora (*e.g.* Nihlgard, 1969). However, since these temperature and humidity regime variations can be expected to be correlated with light regimes (Barkman, 1992), understory light can be used as a single synthetic factor grouping less apparent microclimatic variations.

Understory species vary in their optimal light requirement, or heliophilia. Some ecological classifications of plants are based on this feature: Rameau et al. (1989) distinguished heliophilous, semi-heliophilous and shade-tolerant species, while Ellenberg et al. (1992) classified vascular species along a gradient of nine light indicator values.

Overstory transmittance depends on many tree species properties such as spatial arrangement of leaves (Horn, 1971; Planchais and Sinoquet, 1998), leaf size (Barkman, 1992) and (or) optical properties of leaves, which can be approximated by variables such as canopy closure or leaf area index (LAI).

Table 3
Effect of tree mixing on understory vegetation diversity ("BA": basal area in m^2 ha^{-1}; density is in stems ha^{-1}; all mixing gradient is taken into account (from 0 to 100% of the hardwood species and from 100 to 0% of the coniferous species) except when otherwise stated or symbol "(§)" which signifies unknown)

Reference	Hardwood species	Coniferous species	Understory descriptor	Factor	Relation	Significance
Lücke and Schmidt (1997)	*Fagus sylvatica*	*Picea abies*	Bryophytes SR	*Picea* % cover	+	(*)
			Herbaceous SR	*Picea* % cover	+	*
Ewald (2000)	*Fagus sylvatica*	*Picea abies*	Vascular + bryophytes SR	*Picea* % cover	+	*
			Vascular + bryophytes *H'*	*Picea* % cover	−	ns
			Vascular + bryophytes *E*	*Picea* % cover	−	*
			Ferns SR	*Picea* % cover	+	ns
			Gramidoids SR	*Picea* % cover	+	ns
			Herbs SR	*Picea* % cover	+	ns
			Shrubs SR	*Picea* % cover	+	ns
			Mosses SR	*Picea* % cover	+	***
Simmons and Buckley (1992)	*Quercus* sp.	*Picea abies*	Bryophytes SR	*Picea* BA	?	ns
			Bryophytes SR	*Picea* density	?	ns
			Bryophytes SR	*Quercus* BA	?	ns
			Bryophytes SR	*Quercus* density	?	ns
			Vascular SR	*Picea* BA	?	ns
			Vascular SR	*Picea* density	−	***
			Vascular SR	*Quercus* BA	?	ns
			Vascular SR	*Quercus* density	?	ns
Simmons and Buckley (1992)	*Fagus sylvatica* (§)	*Pinus sylvestris* (§)	Bryophytes SR	*Pinus* BA	?	ns
			Bryophytes SR	*Pinus* density	?	ns
			Bryophytes SR	*Fagus* BA	−	*
			Bryophytes SR	*Fagus* density	−	***
			Vascular SR	*Pinus* BA	+	**
			Vascular SR	*Pinus* density	+	*
			Vascular SR	*Fagus* BA	−	***
			Vascular SR	*Fagus* density	−	***
Helliwell (1978)	*Crataegus oxyacantha, C. monogyna, Berberis vulgaris, Sorbus intermedia, Ulmus glabra, Malus* sp., *Acer platanoides, Tilia cordata, Viburnum opulus, Salix pentandra, Prunus spinosa...* (§)	*Picea* sp. and *Pinus* sp. (§)	Vascular SR (in plantations)	Picea % BA	−	ns
			Vascular SR (in plantations)	Broadleaves % BA	−	ns
			Vascular SR (in old forests)	Picea % BA	+	ns
			Vascular SR (in old forests)	Broadleaves % BA	+	ns
			Vascular SR (in other forests)	Picea % BA	+	ns
			Vascular SR (in other forests)	Broadleaves % BA	+	**
Jobidon et al. (2004)	*Acer rubrum, A. spicatum, Alnus rugosa, Amelanchier* sp., *Betula alleghaniensis, B. papyrifera, Cornus stolonifera...*	*Picea mariana* (and *Picea glauca, Abies balsamea, Thuja occidentalis*)	Vascular SR	*Picea* % BA	max. at 57.6%	***
			Vascular *H'*	*Picea* % BA	max. at 56.7%	***
Lewin (1973)	*Acer saccharum, Fagus* sp., *Tilia* sp., *Liriodendron tulipifera, Quercus* sp., *Betula lenta*	*Tsuga canadensis*	Vascular *H'*	*Tsuga* %	−	(*)
Hicks (1980)	*Acer saccharum, Halesia monticola, Aesculus octandra, Fagus grandifolia, Betula lutea, Tilia heterophylla, ...* (§)	*Tsuga canadensis* (§)	Herbaceous *H'*	*Tsuga* % BA	−	?
Williams et al. (1999)	*Fagus grandifolia, Acer saccharum, A. rubrum, Betula alleghaniensis, Prunus serotina,* etc. (§)	*Tsuga canadensis* (§)	Vascular SR	*Tsuga* BA	−	ns
Peterken and Game (1984)	? (§)	? (§)	Woodland vascular SR	Coniferous % area	?	ns
Glenn-Lewin (1977)	? (§)	*Tsuga canadensis* (and *Pinus* sp., *Picea rubens, Abies fraseri*) (§)	Vascular + tree SR	Coniferous % cover	−	?
Berger and Puettmann (2000)	*Populus tremuloides* (43–100% total BA) and other hardwoods: *Betula papyrifera, Acer saccharum, A. rubrum, Quercus rubra, Tilia americana* (0–44% total BA)	*Abies balsamea* (or other boreal conifers) (0–42% total BA)	Herbaceous *H'*	Conifers % BA	+	ns
			Herbaceous *H'*	*Populus* % BA	+	**
			Herbaceous *H'*	Other hardwoods % BA	−	**

Variations in transmittance among tree species can be considerable. For example, in coniferous plantations of similar basal area, Bolstad et al. (1990) measured a LAI for *P. abies* that was twice that of *Larix decidua*. Among other conifers planted at strictly identical stem densities and constant site type, Klinka et al. (1996) measured variations in canopy cover that ranged from 71.6 to 80% for *Pseudotsuga menziesii*, *Chamaecyparis lawsoniana* and *Picea sitchensis* to 42.1–45% for *Abies amabilis*, *A. grandis* and *Thuja plicata*; Canham et al. (1994) observed less than 2% transmittance for *Fagus grandifolia* and *T. canadensis*, but more than 5% for *Quercus rubra* and *Fraxinus americana*. Although tree species and light quantifiers vary greatly from study to study, consensuses emerged on tree species classifications according to transmittance, *e.g.*, *Fagus* sp. < *Betula* sp., and *Picea* sp. ≤ *Pinus* sp. Conversely, results were conflicting in different studies for the relative classification of species such as *Quercus* sp. and *Pinus* sp. (Brown, 1970; Hill, 1979; Bolstad et al., 1990; Klinka et al., 1996; Aubin et al., 2000; Sonohat et al., 2004).

In mixed stands, variations in transmittance are sometimes explained by the relative proportion of one species: in *P. abies–F. sylvatica* stands, total cover decreased and understory light increased with the proportion of *P. abies* (Lücke and Schmidt, 1997); in mixed *F. sylvatica-Quercus* sp. stands, the more abundant *Quercus* sp. was, the lighter was the canopy cover (Härdtle et al., 2003). The development of subcanopy tree species such as *C. betulus* led to a reduction in understory light (Kwiatkowska and Wyszomirski, 1988). To improve transmittance, Schütz (1998) recommended mixing stands with species such as *Betula* sp., *Fraxinus* sp. or *Pinus* sp. which have a sparse canopy during the growing season, or *Larix* sp., which promotes a brighter understory in winter and spring, like hardwoods.

A few studies sought to explain the effects of tree species on understory vegetation through transmittance quantities. Most were indirect, using different light-related ecological groups or light indicator values. Concerning indicator values, Augusto et al. (2003) found that understory vegetation under *Pinus sylvestris* had higher Ellenberg's indicator values for light than understory vegetation under *Quercus* sp. or *P. abies*, although no difference among tree species for transmittance was detected. Using ecological groups, Lücke and Schmidt (1997) showed that understory vegetation was more heliophilous in *P. abies* and mixed *P. abies–F. sylvatica* stands than in pure *F. sylvatica* stands. Some studies underlined the effect of subcanopy. In stands of *Populus grandidentata*, Roberts (1992) noted an understory of shade-tolerant species under a dense subcanopy of *Acer rubrum*, *A. saccharum* and *F. grandifolia*, while mid-tolerant species became dominant without a hardwood subcanopy. In *Quercus* sp. forests, Kwiatkowska and Wyszomirski (1988) reported a decrease in light indicator value with the growth of *C. betulus*.

An important remark was made by Thomas et al. (1999): light-vegetation relationships might be better explained by past light regimes rather than by current light conditions because of the slowness of species pool variations. Consequently, understory vegetation responses to current light transmittance would be stronger in stands that had few variations in past light regimes.

4.1.2. Soil water

Water is another essential resource for vegetation. In French forests, seven groups of species can be distinguished according to their water preference, from xerophilous to hygrophilous (Rameau et al., 1989). Although these classes are somewhat subjective, these empirical descriptors give an idea of the hygrometric preference of understory species. A somewhat more detailed classification (indicator values, from 1 to 9) was proposed by Ellenberg et al. (1992).

Tree species may affect soil water availability by changing (i) amounts of non-intercepted water, (ii) quantity of water absorbed by tree roots, and (iii) spatial distribution of water at the tree scale (trunk and crown). Many studies have focused on comparing amounts of throughfall, stemflow and (or) intercepted water (relative to rainfall) among tree species. In a review of these studies, Barbier et al. (submitted for publication) reported that throughfall is higher under deciduous than under coniferous species, and declines with the successional status of the tree species – from pioneer through post-pioneer to late-successional species. They also found that, among tree genera with enough data, *Picea* sp. (respectively, *Betula* sp.) has lower (resp., larger) throughfall values while *Fagus* sp. (respectively, *Pinus* sp.) has larger (resp., lower) stemflow values.

As regards physiological properties, tree species differ in transpiration rate per unit of soil water content or potential (*e.g.* Ewers et al., 2002; Pataki and Oren, 2003; Bladon et al., 2006). Water uptake by roots is also species-dependent (among other specific features linked to water), and can to some extent be related to root system morphology. A constant variation in root system morphology has been shown for some American tree species according to their status in the succession: the fine roots of late-successional trees, such as *Abies balsamea* and *Picea glauca*, are located at more superficial levels in the soil than those of early-successional *Populus tremuloides* and *Betula papyrifera* (Grier et al., 1981; Gale and Grigal, 1987; Finér et al., 1997; Bauhus and Messier, 1999). In Europe, *F. sylvatica* is known to have denser fine roots than *Quercus petraea* (Leuschner et al., 2001) or *Pinus sylvestris* (Curt and Prévosto, 2003). By their potential high water absorption, these dense fine roots near the surface may be determining in limiting understory vegetation. However, no study has demonstrated this in the context of tree species comparisons. Studies on the effect of root competition between trees and understory vegetation are relatively numerous (Toumey and Kienholz, 1931; McCune, 1986; Coomes and Grubb, 2000; Lindh et al., 2003; Powell and Bork, 2006); typically, understory species are released from below-ground competition with trees (for water and also nutrients) by cutting trenches. These experiments emphasize the importance of root competition in limiting understory flora (only total cover for most of them), but there are no studies on the relative effects of different tree species.

Nihlgard (1970) attributed the 19% drier soil under *P. abies* compared with *F. sylvatica* to the difference in rainfall interception (39% for *P. abies*, compared with 19% for *F. sylvatica*), but did not test this hypothesis. To our knowledge, no other author has measured soil humidity for tree species

comparison. However, making such comparisons *in situ* may be quite difficult in many situations where an understory vegetation takes up a non-negligible part of the soil water, sometimes more than the overstory trees (*e.g.* Vincke et al., 2005).

4.1.3. Soil nutrients

Plant requirements for soil mineral contents and pH differ among species (*e.g.* Wherry, 1927). Understory species are classified according to soil acidity requirements (Rameau et al., 1989; Ellenberg et al., 1992), and thus understory composition is often used as an indicator of site acidity (Becker, 1988; Brêthes, 1989). Even within each site type, species respond to slight pH variations (Schlenker, 1968).

The effects of tree species on nutrient supply have been reviewed in Europe (Augusto et al., 2002) and the USA (Binkley, 1995). However, irrespective of these differences in nutrient supply, the most useful parameter for understory vegetation may be the resulting soil mineral availability. While some authors (*e.g.* Toutain, 1987) have argued that soil nutrient availability is positively correlated with foliar litter decomposition rate, Prescott (2002) considers that mass and nutrient content of litter produced is the best indicator of soil mineral availability.

Differences in soil mineral content have been noted among tree species (Binkley, 1995; Prescott, 2002). An obvious effect is soil nitrogen enrichment by tree species that have symbiotic relationships with nitrogen-fixing microorganisms, such as *Alnus* sp., *Albizia* sp., *Leucaena* sp., *Acacia* sp. and *Robinia* sp. (Binkley, 1995; Prescott, 2002). Concerning soil pH, it is commonly accepted that conifers produce more acidic topsoil than hardwoods, but this generalization is sometimes wrong. For example, France et al. (1989) measured lower topsoil pH under *Betula papyrifera* and *Acer saccharinum* than under *Pinus strobus* and *Picea glauca*, all planted at the same site. Among hardwoods, *Fagus* sp. and *Tilia* sp. produced more acid topsoil than other hardwoods (Pigott, 1989; Nordén, 1994; Neirynck et al., 2000; Hagen-Thorn et al., 2004).

Soil mineral content may also be influenced by throughfall, as throughfall mineral composition varies with tree species (Parker, 1983; Augusto et al., 2002). Despite geographical variations, there are local and constant differences among tree species. For example, in Europe, atmospheric sulfur deposition under the canopy is two to four times greater than open deposition under *P. abies*, and only 1.2–2.5 times greater under hardwoods (Augusto et al., 2002, reviewing 10 studies). In these studies, we do not know whether these variations in deposition amounts lead to differences in soil mineral content among tree species.

Differences in understory diversity or composition in parallel with tree species composition are often seen as being a consequence of differences in topsoil. In particular, several authors have reported a higher carbon/nitrogen ratio, lower pH and lower nutrient content in coniferous stands compared with hardwood stands, or with an increasing proportion of conifers in mixed stands as explanations of tree species effects (Hicks, 1980; Brown, 1982; Whitney and Foster, 1988; Emmer et al.,

1998; Légaré et al., 2001; Augusto et al., 2003). Bryophytes and herbaceous species often do not have the same responses to these soil modifications. Some authors consider that acidic soil conditions (produced by conifer litter, which is a false generalization, see above) are generally favorable to bryophytes (Harris and Harris, 1997), especially to their cover (*e.g.* Ewald, 2000). In *P. abies* stands, pure or mixed with *Betula* sp., Saetre et al. (1997) explained the lower abundance of bryophytes and the higher abundance of understory vascular species with increasing *Betula* sp. by a gradient of increasing litter pH and topsoil base saturation caused by *Betula* sp. leaves.

Some systematic and ecological characteristics of vascular understory species have been advanced to explain understory composition differences between hardwoods and conifers. Hicks (1980) observed more evergreen species under *T. canadensis*, and Whitney and Foster (1988) observed more ericaceous species under *P. strobus*, compared with hardwood understories. The authors discussed these greater abundances as being a consequence of lower nutrient content in coniferous topsoil. Differences in abundance of acidophilous species – which are more numerous under *P. abies* than under various hardwoods (Teuscher, 1985; Emmer et al., 1998) – have also been logically related to topsoil characteristics. Among the few studies targeted on understory differences between deciduous species, Brown (1982) discussed differences in soil characteristics developed under *Q. petraea* and *Alnus glutinosa* as the factor explaining the differences in understory composition, and Aubert et al. (2004) considered that the more acidic topsoil found under pure *F. sylvatica* compared with mixed *F. sylvatica–C. betulus* explained the higher number of acidophilous species under pure *F. sylvatica* stands.

In lowland European forests, Bürger (1991) and Lücke and Schmidt (1997) found that understory vegetation was richer in nitrophilous species in *P. abies* stands than in *F. sylvatica* stands. By contrast, in mountain forests Emmer et al. (1998) observed fewer nitrogen indicator species under *P. abies* than under *F. sylvatica*. Results varied according to the study location; this could be due to variations in climate, atmospheric pollution level or soil characteristics.

At the tree crown scale, there are variations in abundance of some understory species with distance (not specified) to the nearest stem. Crozier and Boerner (1984) showed that five herbaceous species (out of seven studied) had a mean distance from the stem that varied according to the tree species (*Betula lenta*, *A. rubrum*, *F. grandifolia* and *Quercus alba*). Andersson (1991) found that most species avoided the stem zone of *Quercus* sp. while *Mercurialis perennis* and *Hepatica nobilis* were present around it. Neite and Wittig (1985) observed that base indicator species avoided the stem zone of *F. sylvatica*. These authors attributed the modified plant compositions near the stem to particular mineral soil composition due to stemflow characteristics; solutes in stemflows are known to be more concentrated than throughfalls (Voigt, 1960; Mina, 1965; Edmonds et al., 1991) and alter chemical properties of the soil near the trunk (Gersper and Holowaychuck, 1971), especially by acidifying topsoil (*e.g.* Crozier and Boerner, 1984; Falkengren-Grerup, 1989). This spatial heterogeneity may

cause differences in understory diversity at the crown scale among tree species.

4.2. Other mechanisms

4.2.1. Physical effects of litter

Litter also has physical effects on understory vegetation: seeds under litter are deprived of light and seeds on it cannot root easily (Hamrick and Lee, 1987; Facelli and Pickett, 1991b; Ellsworth et al., 2004). It also has both positive and negative effects on understory development by influencing microclimatic conditions on the floor, such as humidity (Facelli and Kerrigan, 1996; Graae and Heskjaer, 1997) and temperature (MacKinney, 1929; Barkman, 1992; Esteso-Martínez and Gil-Pelegrín, 2004). The nature of this physical effect – positive or negative – on understory vegetation may be non-linear, and reversed above a certain amount of litter (Suding and Goldberg, 1999), and species-dependent.

The amount of soil litter is mainly determined by the balance between litter production and litter decomposition (Staelens et al., 2003). This is influenced by tree species, tree density (e.g. Lebret et al., 2001), site type (Facelli and Pickett, 1991a) and climate characteristics (Bray and Gorham, 1964). Litter weight is also directly dependent on microbial and faunal soil communities. In addition, these communities may be tree species specific. Little characterization has been carried out, but Bezkorovaynaya (2005) showed high variation in soil invertebrate species richness and composition between *Pinus sibirica*, *P. sylvestris*, *Larix sibirica*, *P. abies*, *Betula fruticosa* and *Populus tremula*. These faunal and microbial communities may provide a mechanism by which the overstory indirectly influences the diversity of the understory.

Augusto et al. (2002) reviewed studies on litter weights in Europe. Data showed that they ranged by a factor of 1.7–5.2 among tree species compared in pairs, with *F. sylvatica* < *P. abies*, *Q. petraea* < *P. abies*, *Quercus robur* < *P. abies*, *Q. robur* < *P. menziesii* and *Q. robur* < *F. sylvatica*. A constant trend is higher litter mass under conifers than under hardwoods. Binkley (1995) also reviewed this in the USA. *Alnus rubra* seemed to have higher litter mass than *P. menziesii*, but for other tree species which were compared in more than two studies (*Pinus resinosa*, *P. strobus* and *P. abies*) tree rank according to litter mass varied among studies.

Several litter removal experiments – focused on some particular understory species – showed the inhibitor effect of litter depth on vegetation biomass (e.g. Sydes and Grime, 1981a) or germination rate (e.g. Holderegger, 1996). This negative effect may be at least partly due to the physical effect of litter thickness (Sydes and Grime, 1981b). Ground flora species differ according to their ability to penetrate litter (Sydes and Grime, 1981a). Graae and Heskjaer (1997) observed that *Lamiastrum galeobdolon* and *Oxalis acetosella* are able to penetrate litter layers, whereas *Ficaria verna* and *Poa trivialis* are not; Sydes and Grime (1981b) experimentally observed a negative relation between shoot biomass of *Holcus mollis* and *P. trivialis* and the specific weight of litter applied to them, while *Endymion non-scriptus*, *Viola riviana* and *L. galeobdolon*

yields were insensitive to litter type (litter from four deciduous species, with a factor of 10 between extreme weights).

Penetrating litter requires energy; we can therefore suppose that the more reserves the seed has, the more easily it can get through deep litter. This ability to penetrate litter has been linked to several ecological characteristics: thick litter may impact on the development of acaulescent plants with evergreen leaves (Whitney and Foster, 1988), or annual species compared with perennial (Monk and Gabrielson, 1985). Bryophyte species are more sensitive to the physical effects of litter than vascular species (Hill, 1979). Ewald (2000) explained the higher abundance of mosses under *P. abies* relative to deciduous by the fact that they can survive on a relatively large amount of litter simply by creeping on the litter without contact with the mineral soil layer, but are disadvantaged by relatively large deciduous leaves due to their slow growth rate, which makes them sensitive to covering.

Among the studies comparing understory diversity of the whole community, several authors suggest that the effect of tree species on understory diversity may result from differences in litter thickness among tree species (Emmer et al., 1998; Simmons and Buckley, 1992; Augusto et al., 2003) but this has not yet been proved experimentally.

4.2.2. Phytotoxic compounds

In forest ecosystems, phytotoxic substances that may affect understory vegetation are contained in water running down through the canopy and in the litter (e.g. Helliwell, 1982; Stewart et al., 1984), or directly in the soil for substances released by tree roots (Bertin et al., 2003). They are chiefly water-soluble phenolic compounds (Lodhi, 1976; Becker and Drapier, 1985), which may have negative effects on germination and (or) root development of some species (Beck et al., 1969; Heisey, 1996; Pellissier and Souto, 1999).

The abundance and composition of potential phytotoxic substances depend on tree species (Coulson et al., 1960; Kuiters and Denneman, 1987; Souto et al., 1994). This abundance in the topsoil may be inversely related to litter decomposition rate (e.g. Hagen-Thorn et al., 2004), from which we could argue that coniferous litter may be more toxic for the understory than that from deciduous trees.

Tree allelopathic effects on understory vegetation have been studied on a few species, mostly on tree seedlings in the context of regeneration (e.g. Becker and Drapier, 1984; Facelli, 1994). The following three studies focused on herbaceous species. Lodhi (1976) found that *Acer pseudoplatanus*, *Celtis occidentalis*, *Q. rubra*, and *Q. alba* reduced seed development of two studied herbaceous species, while *Ulmus* sp. did not (in stands with fixed light availability, amounts of most mineral elements and soil pH); the author attributed this effect to growth inhibitors. Pigott (1990) planted *L. galeobdolon* in pots with fixed light intensity in topsoil of *Larix* sp. (with or without addition of $CaCO_3$ to correct pH) or *Quercus* sp. Growth was significantly smaller in *L. decidua* topsoil; the author interpreted this to be the action of growth inhibitors in topsoil under *Larix* sp. Souto et al. (1994) investigated litter toxicity of four tree species on *Lactuca sativa* seeds; a toxic effect of leaf

litter solution was noted with *Eucalyptus globulus* and *Acacia melanoxylon* and not with *Q. robur* and *Pinus radiata* solutions.

Allelopathic *in situ* studies are scant. Daubenmire (1930) and Beatty (1984) pointed out the allelopathic effect of *T. canadensis* to explain the global lower understory SR compared with deciduous stands, without demonstrating this experimentally. This is particularly difficult to do for various reasons such as isolating the potential active substance from others in the soil, and because soil microbes can play a key role in altering allelochemicals (Kohli et al., 2001).

5. Discussion

From the reviewed papers, we can conclude that it is very difficult to make generalizations on the effect of tree species on understory diversity or to establish consensual mechanisms by which tree species can act. Results ranged widely and were sometimes conflicting. This may be partly due to other factors not taken into account in most studies, especially those related to site characteristics and management practices. These are discussed below, and perspectives to improve studies of the effects of tree species on the understory are proposed.

5.1. Difficulties encountered in studies comparing tree species

5.1.1. Site type and characteristics

Tree species depend on site characteristics. In managed forests and plantations the dominant tree species is usually chosen by foresters according to site type; in natural regeneration patterns, tree species composition depends on climate, soil characteristics, disturbance regimes and seed bank composition. For instance, tree SR can be influenced by soil moisture (Hicks, 1980), and tree mixing degree is often explained by topographic characteristics, especially in uplands where the percentage of conifers is positively correlated with elevation (Glenn-Lewin, 1977; Hicks, 1980; Emmer et al., 1998). Understory vegetation is also highly dependent on these site characteristics. Consequently, observed links between overstory and understory (in composition or diversity) are not necessarily causal since understory and overstory may both respond in parallel to site type, as suggested by some authors (McCune and Antos, 1981; Berger and Puettmann, 2000; Légaré et al., 2001).

It would thus be interesting to know whether tree species effect is constant regardless of the site type. Generally, the site type effect is removed by comparing neighbouring stands established on a fixed site type (*e.g.* Brown, 1982), or its variability is unfortunately not taken into account in studies on a larger spatial scale where only the mean response of understory vegetation to tree species is considered (*e.g.* Kirby, 1988; Simmons and Buckley, 1992; Augusto et al., 2003).

5.1.2. Stand management and forest characteristics

Many stand characteristics and practices associated with stand management can affect understory vegetation, such as forest age, total tree abundance, and the preservation of sub-canopy trees.

Forest age was shown as influencing the chemical and structural properties of soil, and consequently understory vegetation (Honnay et al., 1999; Dupouey et al., 2002). This may obscure tree species effects. For example, Whitney and Foster (1988) observed that the age of New England forests – more than or less than three centuries – affected understory composition more than overstory composition (though summarized as conifers or hardwoods). Even so, forest age was not systematically mentioned in the studies on tree species effects that we review (but see Emmer et al., 1998).

For a given tree species, numerous studies have pointed out the negative effect of tree abundance (quantified through basal area or stem density, or directly by light availability) on understory vegetation cover or diversity (Alaback and Herman, 1988; Thomas et al., 1999). This effect can be considerable and may thus bias tree species effect: an abundant overstory can suppress almost all understory species, and a very open overstory can reduce SR by favoring invasive species, as observed for example in *Larix* sp. stands varying in basal area (Balandier et al., 2006). Tree abundance is influenced by stand age and thinning intensity, itself generally driven by silvicultural guidelines for tree species. Hence the diversity of understory vegetation can sometimes be more closely related to silviculture operations than to tree species itself. In studies on tree species effects, authors sometimes seek to control stand age (*e.g.* Brown, 1982) or mean basal area (*e.g.* Berger and Puettmann, 2000). However, these variables cannot be set jointly, as tree species differ in their rotation times—especially conifers compared with hardwoods, or early-successional compared with late-successional tree species. Tree abundance, which is not systematically notified in the studies in Tables 1, 2 and 3 (*e.g.* Skov, 1997; Brunet et al., 1996), has to be taken into account in some way when studying tree species effects (cf. Section 5.2.3).

The preservation or absence of a subcanopy layer greatly modifies understory vegetation (Nagaike et al., 1999), especially by modifying understory light (cf. Section 4.1.1). For example, Kwiatkowska (1994) noted a drastic decrease in understory SR with the development of *C. betulus* in the subcanopy of *Quercus* sp. forests.

Globally, information on forest management is partial and very heterogeneous among studies. More precise indications on past land use (especially former agricultural land or forest land), forest history (forest 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) and tree abundance, by species (*e.g.* Reich et al., 2001) and by class of diameter, would be useful for clarifying how a tree species acts through specific management practices.

5.1.3. Mechanisms

The interacting nature of the factors involved in plant diversity as controlled by tree species has often been underlined (Whitney and Foster, 1988; Berger and Puettmann, 2000;

Harrington et al., 2003). Especially noteworthy are the correlations between light, throughfall and litter amounts, which fluctuate with canopy density (Hill, 1979). Interactions have also been shown to occur among species response to one factor and the level of another factor; for example a lower resistance of vegetation to shade parallel to soil acidification has often been mentioned (Moir, 1966; Mitchell and Kirby, 1989; Portsmuth and Niinemets, 2007). Because of these interactions, the analysis of factors taken individually may lead to erroneous interpretations of the mechanisms involved (cf. Section 5.2.1). We should keep in mind the various potential influencing factors and envisage interacting effects among them to explain the response of the different ecological groups to the tree species effect. It is especially important to carry out experiments paying careful attention to factors other than those actually under study, as did Pigott (1990), who demonstrated the implication of allelopathic substances by setting light quantity and controlling topsoil composition and pH. Although the mechanisms cited in Section 4 are often mentioned in discussions to explain tree species effect, they have rarely been treated as working hypotheses.

5.2. Perspective: improving statistical analysis of the link between biodiversity and tree species composition

More consideration should be devoted to the development of statistical models to analyze the relation between tree species composition and selected parts of understory vegetation biodiversity. Below, we stress three points in particular: (i) the choice of the level at which biodiversity should be analyzed, (ii) the choice of the general structure of the statistical models—linear or non-linear, with or without random effects, probability distributions underlying the model, etc., and (iii) the choice of the way in which ecological variables are incorporated into the model.

5.2.1. Level of biodiversity

We believe that it is important to take a pluralistic view of the analysis of biodiversity response to tree species composition, because composition differences may occur even when total diversity does not change. Detecting responses at the species, ecological group and global levels is particularly important (Gosselin and Gosselin, 2004). Different techniques can be used here, including multivariate analyses (e.g. Légaré et al., 2001) and parametric or non-parametric analyses of the diversity of subgroups based on ecological characteristics (e.g. Lücke and Schmidt, 1997), indicator values (e.g. Augusto et al., 2003), or presence/absence or abundance of species (e.g. Peterken and Game, 1984; Ewald, 2000). Following Gosselin and Gosselin (2004), we consider only parametric models below.

Ecological groups may have a central role, helping to explain the mechanisms behind the tree species-biodiversity relation. Ecological groups defined by the relationship between floristic species and a particular mechanism – for example the heliophilous character of understory species – would make it possible to indirectly test hypotheses on the importance of the mechanism in this relation. This can be done at the level of the ecological group, as in references quoted in Section 4.1.1, or at the species level, as in Thomas et al. (1999), Richard (2004) or Gelfand et al. (2005).

This does not preclude testing hypotheses based on other ecological classifications of species. For example, boreal, mountain and vernal species should be favored by hardwoods, which have a colder understory in winter and more light in spring than conifers (Roussel, 1972; Mitchell and Kirby, 1989; Pigott, 1990; Barkman, 1992; Harris and Harris, 1997). By contrast, among deciduous species, trees such as *Betula* sp., which have early bud break and early leaf fall, have a light regime favorable to bryophytes, while *Quercus* sp. has a light regime favorable to geophytes (Barkman, 1992). It is also possible to distinguish understory species according to their successional status, using a hypothesis that specifies the different response of successional understory ecological groups to the successional status of the dominant tree species (building on Auclair and Goff, 1971).

5.2.2. General structure of statistical models

Statistical models used to analyze biodiversity-tree species relations in the past were limited by (i) the probability distributions used in the model—most models were based on Gaussian distribution, (ii) the linearity of the model, and (or) (iii) non-allowance for the structure of the sampling design in the analysis. The more the analyses target specific groups or species (cf. Section 5.2.1), the more we need non-linear statistical models (Austin, 2002). In their statistical models analysts should use probability distributions restricted to non-negative values for most biodiversity quantifiers. They should also consider incorporating the sampling structure – especially the spatial structure – in some way (e.g. through data transformation based on summaries at the level of spatial clusters, cf. Augusto et al., 2003, or by using random effects accounting for spatial structure of the data). The previously mentioned lack of statistical tests on the biodiversity-tree species link (cf. Section 3.1) may be partially accounted for by authors' difficulty in developing statistical models with an adequate structure.

5.2.3. Choice of the ecological model

An additional improvement in statistical models could be achieved by the way ecological models are formulated. For example, instead of analyzing only the effect of the identity of the dominant tree species (as in Tables 1 and 2), we can analyze the combination of identity of dominant tree species and centered stand abundance. This would account for effects of varying stand density inside each tree species category (cf. Section 5.1.2). Also, if we believe that absolute abundance is a key variable in shaping floristic biodiversity, we could replace the analyses in Table 3, in which only one variable (abundance or relative abundance of one tree species) is used in the regression, by a model in which the combination (linear or nonlinear) of abundances of both species is incorporated (e.g. Gosselin and Barbier, 2005). Another alternative would be to integrate a combination of total abundance and relative

abundance or presence/absence of a tree species (cf. Saetre et al., 1997). This kind of choice can change the significance or the direction of the results. For example, Saetre et al. (1997) observed that the effect on vegetation abundance of *Betula* sp. presence in *P. abies* stands appeared only when the model was adjusted to total stand basal area, a measure of tree absolute abundance. These approaches may be limited by correlations between factors.

Concerning site type, we can (i) work within a restricted site type variability and compare models of tree species effect among site types or (ii) work on datasets with various site characteristics and include them as co-variables in the models, or even try to develop models where site characteristics interact with tree species effects, if there is enough data.

6. Conclusion

Tree species effect on understory vegetation diversity and composition between conifers and hardwoods has often been compared and discussed, whereas studies among coniferous species or deciduous species are scarcer. In addition, few statistical tests have been performed in these studies. We must be careful when reducing tree species effect to a ''coniferous'' or ''hardwood'' effect. The study of the mechanisms show that the two groups intersect in the classification of tree species according to light interception, for example, and species such as *Pinus* sp. or *Larix* sp. can have a more diversified understory than some hardwood species. Although tree SR is nowadays promoted to favor understory diversity, it has rarely been a subject of study. Also, there are indications that in many cases, monospecific stands would be more favorable to biodiversity than two-species mixed stands, insofar as SR or H' are considered.

The mechanistic approach enables us to build hypotheses for the different responses of understory species to various tree species. However, further experimental studies *in situ* are needed, and we must pay close attention to avoid confusing interpretations of the mechanisms involved because of their interacting nature.

When comparing tree species, we must be careful to allow for the effects of site type and stand management practices, because these factors may add variability to tree species effects on understory vegetation, or may even be the main factors. We should accurately control these factors before concluding on potential tree species effects, either by taking into account site and management variability in the models, or by setting site and management characteristics and so investigating tree species effects in a specific ecological forest context. Finally, we advocate using special care to determine the structure and content of the statistical models used to analyze the relation between tree species and floristic biodiversity.

Acknowledgments

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