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Managing tree species diversity and ecosystem functions through coexistence mechanisms

Thomas Cordonnier¹ · Georges Kunstler¹ · Benoît Courbaud¹ · Xavier Morin²

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Abstract

• **Key message** A better transfer to managers of studies examining the functional role of tree species diversity would be achieved by explicitly addressing two missing links: the effect of management interventions on coexistence mechanisms and the relationships between coexistence mechanisms and ecosystem functions.

• **Context** Plant species diversity has been shown to promote a wide array of ecosystem functions and ecosystem services. However, scientific results concerning relationships between species diversity or species mixing and ecosystem functions have not been well transferred to management practices so far. Part of the problem lies in the difficulty of assessing whether interesting species mixtures can persist over the long term and how management influences ecosystem functions.

• **Aims** We argue that a better transfer of knowledge to managers would be achieved by addressing two missing links: (i) the effect of management interventions on coexistence mechanisms and (ii) the relationships between coexistence mechanisms and ecosystem functions.

• **Methods** To do so, we first provide a brief overview of the recent scientific results on relations between tree diversity (or two-species mixing) and ecosystem functions, focusing on studies dealing with productivity and stability in forests. We further introduce the key question of whether mixed stands are transient or permanent. We then briefly present key elements of modern coexistence theory and illustrate them with three examples in forest ecosystems. We finish by discussing how management interventions in forests can affect coexistence mechanisms and by addressing some methodological perspectives.

• **Results** We provide examples of management actions (e.g. gap-based silviculture, preferential selection of the most frequent species, preferential selection of the most competitive species, planting weakly competitive species) that may increase the strength of coexistence mechanisms.

• **Conclusion** Analysing long-term management impacts on species coexistence and ecosystem functions with a combination of long-term monitoring of large permanent plots and mechanistic dynamic model simulations will be useful to develop relevant practices favouring mixed forests in the long term.

Keywords Stability · Productivity · Species coexistence · Forest management · Diversity effects

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Contribution of the co-authors TC conceived the original idea and wrote the first draft. GK and XM refined the design of the paper and contributed significantly to the writing. BC participated in the design of the paper and carefully read, criticised and edited the last versions of the paper.

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1 Introduction

There is growing consensus that species diversity within a plant community promotes a wide array of ecosystem functions and services (Cardinale et al. 2012; Isbell et al. 2011; Pasari et al. 2013). Studies have advanced our understanding of how abiotic and biotic factors influence the relationship between species diversity and ecosystem functions. This paves the way to a new approach to ecosystem management that aims to maintain and promote multispecies or functionally diverse communities to support resource production and other ecosystem services (e.g. pest control, recreation, protection against natural hazards) (Duru et al. 2015; Mori et al. 2017).

Regarding forests, positive effects of tree species diversity on ecosystem functions and services have been reported in numerous studies (e.g. Gamfeldt et al. 2013; Jucker et al. 2014; Liang et al. 2016; Van Der Plas et al. 2016; Zhang et al. 2012), mostly focusing on mean productivity and its stability (temporal stability, resistance and resilience). Beyond the species diversity effect, several authors have also outlined that specific species mixtures (especially two-species mixtures) can have a higher stability or productivity than corresponding mono-specific stands (Forrester and Bausch 2016). For forest managers, the reasons for maintaining or promoting multispecies stands are multiple, from provisioning specific servicing functions within silvicultural systems (e.g. trainer species, Bausch et al. 2016) to enhancing the aesthetics of landscapes for recreational activities or preserving specific microhabitats for biodiversity conservation. However, the positive effect of species mixing on ecosystem functions has greatly renewed interest in the management of mixed forests and their maintenance, especially in the context of climate change.

The difficulty of defining management guidelines for maintaining mixed stands has been highlighted by practitioners (Coll et al. 2018). For instance in European forests, a classical example is the difficulty of achieving sustained overyielding in *Quercus petraea*–*Fagus sylvatica* stands (Pretzsch et al. 2013a) in which shade-tolerant beech gradually dominates the shade-intolerant oak (Von Lüpke 1998; Bausch et al. 2016). Similar difficulties arise in other European forests involving codominance by shade-tolerant and shade-intolerant species such as *Pinus sylvestris*–*Fagus sylvatica* and *Abies alba*–*Picea abies* stands (del Río et al. 2017; Vallet and Pérot 2011). In western Canadian boreal forests, overyielding mixed stands of *Populus tremuloides*–*Picea glauca* (Man and Lieffers 1999) also follow a succession to *Picea glauca* dominance in the absence of major disturbance (Kabzems et al. 2016). Such observations call into question the feasibility of species diversity-based management if mixtures favourable for ecosystem functions are naturally transient and require substantial intervention to maintain species coexistence. Moreover, even if mixed stands can be maintained through management, the consequences on ecosystem functions are difficult to anticipate (Bausch et al. 2016), given that management

practices deeply modify interactions between species, as well as recruitment processes in space and time.

In this article, we argue that mixed species forest management needs to be rooted in a better understanding of (1) species coexistence mechanisms and the way they are influenced by management interventions and (2) the relationships between coexistence mechanisms and ecosystem functions. The first point is essential to understand which mixtures of tree species are transient (one or several species of the mixture likely to be lost in a period shorter than one harvest rotation) or permanent (species coexist for more than one rotation, although their relative abundance can fluctuate; minor species can appear or disappear) and how management can influence species coexistence. The second point is required to quantify the joint impact of species mixing and management on ecosystem functions. Improving our knowledge on these two aspects would help managers assess the value of working for species coexistence instead of accompanying the natural dynamics that can possibly lead to monospecific situations.

To do so, we first provide a brief overview of the recent scientific results on links between tree diversity and ecosystem functions. We further provide several examples of the potential and limits for forest management, highlighting the key question of whether mixed stands are transient or permanent. We focus specifically on productivity and stability functions because these are great examples of the duality between stands that are “functionally interesting” and “difficult to manage” and because ecological studies mainly addressed these two fundamental functions. To better understand how management actions can impact species coexistence, we need to consider current coexistence theory and synthesise its connection to ecological processes and ecosystem functions. Hence, we briefly present key elements of modern coexistence theory and illustrate them with three examples in forest ecosystems. We then discuss how management actions in forests can affect coexistence mechanisms. We finish by presenting some methodological perspectives.

We focus on the relationships between tree diversity and ecosystem functions at the local scale (stand to management unit) as studies dealing with productivity and stability have been most frequently conducted at this level, and because this is the scale at which silvicultural trials usually occur. However, we will consider coexistence mechanisms that can operate at larger scales (landscape) and finer scales (tree–tree interactions) because they can influence species coexistence at the stand or management unit level.

2 Productivity and stability in forests

2.1 General results and utility for management

In mixed forests, both the mean level and the stability of productivity are usually greater than in monospecific stands

(Jucker et al. 2014; Liang et al. 2016). Many studies also provide specific examples of mixed-species stands that overyield (i.e. increased mean productivity in mixed stands in comparison to standardised monospecific stands) and/or have higher stability of productivity (i.e. decreased interannual variation in productivity in mixed stands). For instance, Toïgo et al. (2015) reported the higher productivity of two major mixed-forest types in Western Europe, *Quercus petraea*–*Fagus sylvatica* and *Picea abies*–*Abies alba*. In boreal forests, the very widespread mixture of *Populus tremuloides* and *Picea glauca* is considered to be favourable to productivity (Man and Lieffers 1999). Regarding stability, del Río et al. (2017) found higher temporal stability in mixed *Pinus sylvestris*–*Fagus sylvatica* stands than in corresponding monospecific stands. This positive effect seems to hold for other facets of stability, such as resistance or resilience to disturbance. For instance, it has been shown that the growth of both *Fagus sylvatica* and *Abies alba* can gain in resistance and resilience to drought (i.e. time needed for recovery after a drought event) when mixed with other species such as *Picea abies* or *Quercus petraea* (Lebourgeois et al. 2013; Pretzsch et al. 2013b).

The magnitude of the mixing effect depends on factors that are important for silviculture and planning: species identity, stand density, forest development stage, climatic conditions and site quality (Forrester and Bausch 2016). Usually, the harsher the growing conditions, the greater the magnitude of the positive effect of mixing or diversity on productivity and stability (Lebourgeois et al. 2013; Toïgo et al. 2015). Humpback-shaped relationships are expected between the strength of the diversity effect and stand density because high densities favour competition that can outweigh complementary interactions between species, while low densities tend to weaken interactions that trigger complementarity (Forrester 2014). Similarly, stand age can also modulate diversity–productivity relationships through changes in competition intensity and structural diversity (Forrester 2014; Zhang et al. 2012).

Mechanisms responsible for the positive effects of diversity on ecosystem functions have been discussed by several authors (Forrester and Bausch 2016; Jucker et al. 2014; Morin et al. 2014). When overyielding on mean productivity is observed, it may be due either to strong complementarity effects (those leading to an increase in the performance of mixed communities above that expected from the performance of individual species, including resource partitioning and/or decreased competition effects) or to selection effects (measured by the covariance between the performance of species in monospecific stands and their relative change in performance in mixture, thus related to species dominance in the mixed stands, including the sampling effect) (Loreau and Hector 2001; Loreau 2010), while increased stability in productivity appears to be related to the asynchrony in species' response to environmental conditions (Jucker et al. 2014), a temporal complementarity effect. All these mechanisms invoke many processes

implicated in complementarity effects such as species differences in light interception, light use efficiency and differences in exploitation of water and nutrient resources and in responses to environmental fluctuations. Yet, these processes can rarely be quantified in field studies, and our understanding of the underlying mechanisms remains limited.

2.2 The persistence issue

A key question for forest managers that has not been thoroughly explored is whether mixed stands, reported to have higher stand productivity or stability than pure stands, will persist over time, i.e. whether the positive effect of diversity will be maintained over the long term or will only be transient. Most experiments in forests are still too young to provide direct answers (Scherer-Lorenzen 2014). Based on experiments at the local scale in grasslands, it seems that species-rich assemblages have, in general, persisted throughout the duration of the experiment (Hector et al. 2007), and the positive effects of diversity have generally increased with time (Cardinale et al. 2007; Reich et al. 2012), mainly because of an increased complementarity effect (Fargione et al. 2007). These experiments may have, however, included weeding and/or re-planting to maintain the mixture.

Results in forests are much less clear, perhaps due to the lack of experiments testing long-term coexistence. First, at the stand scale, numerous studies reported overyielding for species mixtures that are generally considered transient, such as mixtures of early- and late-successional species (Cavard et al. 2011; Pretzsch et al. 2013a; Pretzsch et al. 2015). This finding is consistent with the hypothesis that overyielding can be asymmetrical (Toïgo et al. 2015), i.e. benefitting more shade-tolerant species (Toïgo et al. 2018) that will competitively displace less shade-tolerant species in the long term. However, this asymmetry is not the rule: some studies also found a positive response of all species in the mixture (e.g. Collet et al. 2014 for *Fagus sylvatica*–*Acer pseudoplatanus*). Then, the few studies that analysed how the strength of the biodiversity effect changes along succession in forests have reported a decrease of this effect over time that can result from either competitive exclusion of a set of species or from changes in the strength or direction of complementarity effects (Caspersen and Pacala 2001; Lasky et al. 2014). Only one study (Guerrero-Ramirez et al. 2017) found consistent effects of species diversity on basal area increment over time in experiments covering a few decades. Therefore, maintaining mixtures and their positive effects on ecosystem functions at the stand scale or the management unit level can be challenging, particularly in temperate forests where the level of diversity is intermediate.

The practical question arising from the preceding points is how management interventions can facilitate the persistence of an overyielding or more stable species mixture in the long term. We believe that connecting management with the

analysis of species' competitive differences and the ecological theory of coexistence (Chesson 2000b; HilleRisLambers et al. 2012) would allow developing more general management guidelines for mixed stands. Hence, in the next sections, we briefly introduce coexistence mechanisms, provide three examples and then discuss how management interventions can potentially modulate the effects of coexistence mechanisms.

3 Coexistence mechanisms

3.1 Coexistence theory

Modern coexistence theory is based on mathematical equations relating the mean low-density growth rate of a species to the effects of competition and the environment in ecological communities (Chesson 1994, 2000a; Barabás et al. 2018). The main originality of Chesson's theory is that it teases apart coexistence mechanisms that emerge in fluctuating (temporal or spatial) and non-fluctuating environments (Chesson 2000b). This theory embeds multiple scales, from local interactions between individuals to spatial scales where dispersal is limiting for species and from 1 year to temporal scales where effects of environment fluctuations on species demography becomes tangible (e.g. several decades for trees).

In non-fluctuating environments, coexistence is driven by two different components: one based on differences in species fitness (ratio between the mean per capita growth rate of the species in the absence of resource limitation and the rate at which its per capita growth rate declines as resources decline in abundance) and the other based on species niche overlaps, which is related to the relative importance of intraspecific and interspecific competition.

In Chesson's theory, *equalising mechanisms* refer to ecological processes that limit the differences in fitness between co-occurring species. If a species has a large fitness disadvantage in a given environment, the species will be excluded by other species better suited to the environment. Equalising mechanisms promote coexistence by reducing this difference. This is an unstable coexistence mechanism given that, without niche differentiation of species (i.e. species use resources differently), species cannot coexist in the long term: competitive exclusion occurs and in the end only one species remains. Reducing fitness differences slows down competitive exclusion and can lead to apparent coexistence on a short time scale. *Stabilising mechanisms* promote coexistence by increasing **intraspecific competition** relative to **interspecific competition**, which leads species to perform better when rare. These mechanisms, which are caused by niche differentiation of species, are considered stable because they allow infinite coexistence of species. Figure 1 (adapted from Adler et al. 2007) presents a theoretical diagram illustrating how hypothetical mixed stands can be either transient in the competitive exclusion zone or stable in the

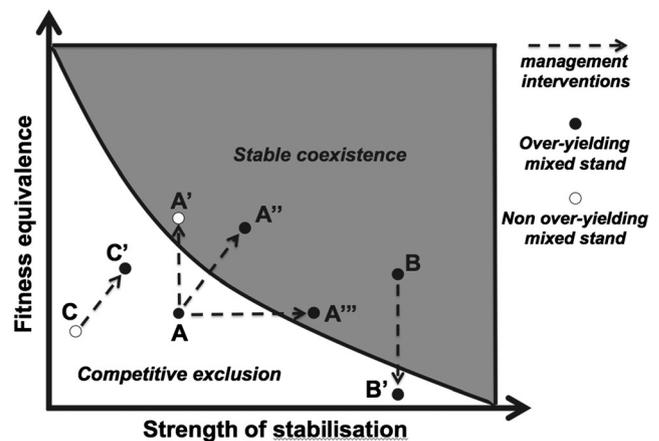


Fig. 1 Diagram showing how hypothetical mixed stands are either transient in the competitive exclusion zone or stable in the coexistence zone in the space of fitness equivalence and strength of stabilisation and the various potential effects of management on these stands. We also present hypothetical management interventions that can move (dashed arrows) a transient stand (A) into the coexistence zone by either changing the fitness equivalence (A', for instance by cutting preferentially the most competitive species) or the strength of stabilisation (A'', for instance by preferentially cutting the most common species) or both (A''', for instance by applying gap silviculture adapted to species requirements). But management interventions can also move a stable coexisting mixed stand into the competitive exclusion zone (pathway B–B', for instance by harvesting preferentially one of the species) or may not be efficient enough to stabilise a mixed stand (pathway C–C'). In addition, management interventions can also impact the positive effect of biodiversity on ecosystems' function (for instance the overyielding), either decreasing it (A') or increasing it (C'). In general, depending on the species involved, management interventions can affect both stabilising and equalising mechanisms, as illustrated by moving from mixture A to A'', but with different intensities. It is important to point out that the two dimensions of the diagram are difficult to quantify and to tease apart in field studies

coexistence zone in the space of fitness equivalence (equalising mechanisms) and strength of stabilisation (stabilising mechanisms).

In a temporal fluctuating environment, stable coexistence is made possible by four additional phenomena: (i) the response of species growth rates to competition are non-linear and differ between species (*relative non-linearity*), (ii) the response of species' growth rates to environment fluctuations differ between species (*species asynchrony*), (iii) the covariance between environment and competition effects decreases with species abundance and (iv) the response of species' growth rates to competition and environment is non-additive. The last three phenomena form together the *storage effect* which “is a metaphor for the potential for periods of strong positive growth that cannot be canceled by negative growth over time” (Chesson 1994). Chesson extended his theory to spatial variations, which includes a specific coexistence mechanism called *fitness density covariance*, namely a positive covariance between density and favourability in local conditions for individuals of species (Chesson 2000a; Hart et al. 2017).

It is important to highlight that if stabilising mechanisms are essential for stable coexistence, they interact with equalising mechanisms. For instance, in Fig. 1, increasing fitness equivalence by moving from state A to A' makes coexistence possible for a given level of stabilising mechanisms. It is also important to point out that equalising and stabilising mechanisms are emergent properties described by theoretical models' parameters. Defining the ecological processes leading to these mechanisms is a difficult task. For instance, spatial aggregation (or segregation) of species at the juvenile stage is usually considered by forest managers as helping to maintain species mixing (Bauhus et al. 2016). However, in Chesson's theory, spatial aggregation of species per se does not necessarily lead to infinite coexistence of species (Chesson and Neuhauser 2002). Depending on ecological processes that generate it (spatial heterogeneity, seed dispersal, species interactions), the spatial aggregation of species might, however, promote stabilising mechanisms (Murrell et al. 2002, Hart et al. 2017).

In addition, quantifying these mechanisms in plant communities is difficult. Chesson (2008) proposed several ways to do it: (i) studying the response of species (growth, survival, recruitment) to complete competition removal and to different levels of competition, (ii) studying the covariance of environment and competition effects at low and high species densities and (iii) identifying differences in recruitment variability at low and high species densities. Actually, only a few studies have performed this type of exercise in forest ecosystems (Kelly and Bowler 2002; Usinowicz et al. 2017). Despite several obstacles for field applications, Chesson's theory remains one of the most coherent and complete theories of species coexistence and as such deserves to be considered in more applied contexts.

3.2 Three examples of ecological processes influencing coexistence mechanisms

Ecological processes influencing coexistence mechanisms are numerous, and it is beyond the scope of this article to provide a complete overview of them. Here, we present three examples that will also be useful when discussing the effects of management on coexistence mechanisms. The first one deals with species characteristics (trade-offs between life-history traits), the second focuses on the recruitment process (recruitment limitation) and the last one addresses the mortality process (frequency-dependent mortality).

3.2.1 Example 1: trade-off between maximum growth rate and tolerance to competition

Our first example is based on the trade-off between maximum growth rate and tolerance to competition (Kunstler et al. 2009). Early successional species are often characterised by fast growth without competition but low survival and growth rates

under competition, whereas late successional species are often characterised by slow growth without competition but only a slight reduction in survival and growth rates under competition. This trade-off, which is closely related to the successional niche of tree species (Pacala and Rees 1998), appears to be relatively consistent among biomes and is partly related to specific traits such as wood density and specific leaf area (Kunstler et al. 2016). In this example, less competitive species can persist in the landscape because of their higher resource use efficiency in disturbed areas (e.g. higher light and nitrogen) at the juvenile phase. This makes them able to complete their life-cycle before being excluded by more competitive species. This trade-off limits the interactions between species in time and increases local competition between conspecifics, which is an essential feature of stabilising mechanisms for coexistence (Chesson 2000b).

3.2.2 Example 2: recruitment limitation

The second example is related to the recruitment limitation of tree species reported in both tropical and temperate forest ecosystems (Clark et al. 1999; Hubbell et al. 1999). Recruitment limitation can stem from low fecundity, short-distance seed dispersal or lack of safe sites for seedling establishment (Clark et al. 1999). Recruitment limitation reduces the effect of interspecific differences in tolerance of competition by reducing the chance of interactions, which in turn slows down the competitive exclusion process (Chave et al. 2002). When all species are concerned, recruitment limitation can be considered as an equalising mechanism as it tends to flatten fitness differences among species. However, when combined with a competition–colonisation trade-off, recruitment limitation can also lead to stable coexistence of species (Chave et al. 2002). Such competition–colonisation trade-offs can arise from the positive correlation between seedling competitive ability and seed size associated with negative correlations among seed size, seed number and dispersion distance (Henery and Westoby 2001). In this case, the recruitment limitation of competitive species allows fugitive species (i.e. species having good dispersal ability but low competitive ability) to colonise available sites by forfeit (Hurt and Pacala 1995). The predominance of the competition–colonisation trade-off in forests is still discussed however (Clark et al. 2004).

3.2.3 Example 3: frequency-dependent mortality

Predation is an interesting analogy to some forest management interventions. Predation induces “[...] a negative effect on the immediate per capita growth rate of a prey species by consuming part or all of prey individuals” (Chase et al. 2002). Predation thus induces mortality events, which have major effects on species coexistence (Chesson and Kuang 2008). However, the effects of predation on species coexistence are

complex and the same predation process can lead to different outcomes depending on predation intensity and characteristics of prey species (Chase et al. 2002). Nevertheless, predation that leads to the reduction of most common species, i.e. negative frequency-dependent mortality with switching behaviour, can promote coexistence of many species (Chesson 2000b). In forests, a good example of the effect of specialist predators on species coexistence is the Janzen-Connell effect (higher mortality of seeds or seedlings that are near conspecific adult trees due to species-specific enemies; HilleRisLambers et al. 2002), which favours the recruitment of rare species.

3.3 Coexistence mechanisms and ecosystem functions

Despite the key role played by coexistence mechanisms in the long-term dynamics of mixed stands, there is a lack of studies that directly connect coexistence theory to ecosystem functions. Indeed, a key unresolved theoretical question is whether mechanisms that promote species coexistence (Fig. 1 and the examples presented above) are also related to a positive effect of species diversity on productivity or stability. This is central to understanding which species assemblage will persist over time while still providing a strong diversity effect on ecosystem functions. Recently, two studies based on simple models of resource use (Carroll et al. 2011; Turnbull et al. 2013) discussed the relationships between complementarity vs. selection effects in mixtures and the stabilising/equalising mechanisms. Both studies concluded that although complementarity is related to stabilising mechanisms, it does not guarantee the coexistence of species in the long term. In addition, depending on the mechanisms of coexistence at play, higher diversity will not necessarily lead to higher productivity (Kinzig and Pacala 2001). For instance, if coexistence is maintained by successional niche differences (as in example 1), and early successional species are the fastest growing species, then a mixture of early- and late-successional species will have lower productivity than a monoculture of early successional species (Kinzig and Pacala 2001). Future research along these lines will be critical to improve forest management that draws on coexistence theory.

4 Coexistence mechanisms and management

Studies that address ecosystem functions, species diversity and coexistence processes provide relevant perspectives for environmental managers, but in general, these studies remain disconnected from practical management actions, especially in forest ecosystems. To foster this transfer to managers, we need additional research (Fig. 2): (i) explicitly addressing how different management interventions modulate coexistence mechanisms and thus influence the long-term coexistence of species and (ii) quantifying the types and strength of

coexistence mechanisms that affect productivity and stability. Regarding the first issue, Chesson's theory can be relevant to, and even inspiring for, forest managers in two different ways.

First, coexistence theory could help identify ecological situations in which management interventions are needed to strengthen stabilising or equalising mechanisms to ensure coexistence. For instance, in Fig. 1, state B leads to the coexistence of species without any specific management actions, an outcome that corresponds to some situations observed in North American forests (Kneeshaw and Prévost 2006; Poulson and Platt 1996) and European forests (*Fagus sylvatica*–*Acer pseudoplatanus*, *Fagus sylvatica*–*Abies alba*). In this case, the concern is that any weakening of coexistence mechanisms through management interventions could favour competitive exclusion (for instance state B' in Fig. 1). On the contrary, state A leads to competitive exclusion and strong management interventions are necessary to maintain species mixing, as in our earlier example of mixed *Abies alba*–*Picea abies* stands. For other mixed stands (state C in Fig. 1), such as mixed *Fagus sylvatica*–*Quercus petraea*, interventions might not be sufficient (Ligot et al. 2013; Van Couwenberghe et al. 2013; pathway C–C' in Fig. 1) and coexistence can only be achieved at larger scales because of spatial heterogeneity (Hart et al. 2017), by strict control of the most competitive species or through high spatial segregation of the two species (Bauhus et al. 2016).

Second, consideration of coexistence theory could help define the most efficient strategy to maintain a given mix of species. In this regard, better knowledge on whether the forest managers might strengthen equalising mechanisms or stabilising mechanisms is of interest. In Fig. 1, this conundrum is represented schematically by the pathways A–A' and A–A'''. In this case, increasing equalising mechanisms (pathway A–A') may be less efficient than strengthening stabilising mechanisms (pathway A–A''').

To better illustrate these sorts of relationships between management activities and coexistence mechanisms, in the following section, we present examples of interventions commonly used to modify forest structure and dynamics at the stand scale or the management unit level and their potential effects on coexistence mechanisms. This exercise is complementary to the one undertaken by Bauhus et al. (2016), which provides more practical silvicultural recommendations for the management of mixed stands.

4.1 Management interventions in forests

Depending on the silviculture management system, management tempo is characterised by successive (even-aged systems) or simultaneous (uneven-aged systems) application of four main interventions. The first one, called *tending*, consists in a general improvement of the stand at young development stages by reducing tree density and modifying tree

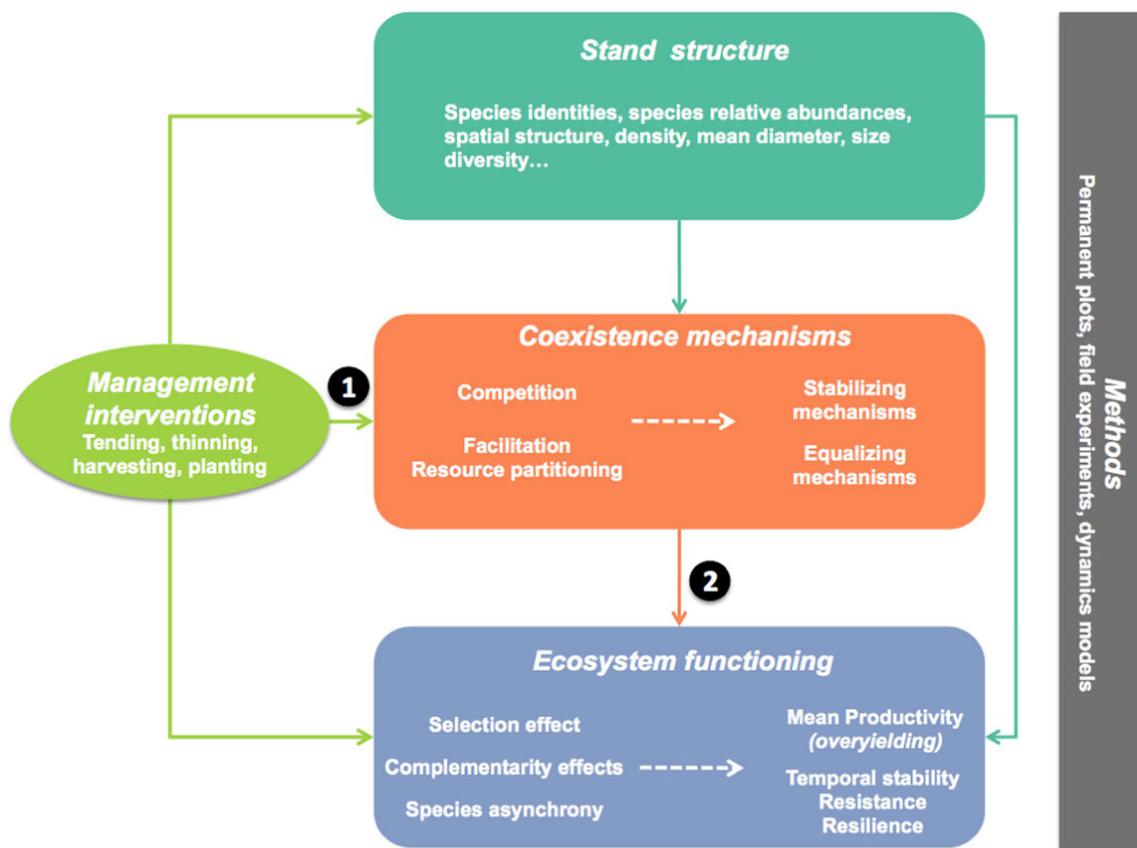


Fig. 2 Diagram illustrating the links between stand structure, coexistence mechanisms, functioning of key ecosystem processes and forest management interventions. We emphasise two links (1 and 2) that are

critically important for future studies to increase our understanding of the potential effect of management on forest ecosystem functions

species' relative frequencies (frequency-dependent selection). The second one, called *thinning*, is similar to tending but concerns more mature stands. Thinning mainly regulates competition between trees by decreasing density (i.e. density-dependent selection). Preferential selection of species is still possible at this stage, although usually considered less efficient. The third intervention, *harvesting*, creates open areas of different sizes depending on the silviculture system considered: tree crown size in the individual selection system, several hundred metres in the group selection system, several hectares for the uniform shelterwood system or up to clear-cuts, which can be very extensive. Harvesting usually leads to regeneration or recruitment pulses (sometimes preceded by soil preparation), either naturally or through a mix of natural regeneration and planting of seedlings: this is the last intervention called *regeneration*. Regeneration is of major importance because this is the step where managers pay particular attention to the acquisition of species mixing. Planting seedlings can be targeted to gaps or in relation to neighbouring trees to increase mixing or density. This type of planting program can either enrich species assemblages or mimic regeneration pulses when the planted species are the same as those of mature trees.

4.2 Illustrating the effects of management on coexistence mechanisms

Management actions regulate both the dynamic of each species and their competitive interactions, thus affecting coexistence mechanisms (Table 1). Some interventions may primarily change the strength of equalising mechanisms. For instance, planting (or favouring regeneration by soil preparation) of a species (i.e. enrichment) can promote or decrease fitness equality depending on the functional characteristics of the species. Planting weakly competitive species (e.g. *Quercus pedunculata*, *Pinus sylvestris*, *Pinus banksiana*, *Populus tremuloides*) should increase their density and thus facilitate their persistence through increased fitness (c.f. Fig. 1, A to A' making coexistence possible). Conversely, planting strong competitors (e.g. *Fagus sylvatica*, *Abies alba*, *Abies balsamea*, *Picea glauca*, *Tsuga heterophylla*) should accelerate the competitive exclusion process by reducing recruitment limitation and thus increasing the chance of interactions with less competitive species (B to B' in Fig. 1). Another good example includes tending and thinning operations that focus on the most competitive species, which reduces the fitness advantage of these species and thus slows competitive

Table 1 Examples of the effects of primary interventions used in forest management on equalising and stabilising mechanisms. The stabilising effect of each intervention is detailed in brackets

Management intervention	Equalising = reduces fitness differences	Stabilising = reduces interspecific competition relatively to intraspecific competition
Regeneration planting* (enrichment)	Increases the abundance of planted species Decreases recruitment limitation of planted species	Increases species density in favourable habitats (favouring the spatial storage effect)
Tending and thinning	Decreases overall density Decreases the abundance of the most competitive species	Decreases the abundance of dominant species (decreasing interspecific competition)
Harvesting	Decreases overall density Modulates structural heterogeneity	Increases resource heterogeneity in space and time (increasing spatial and temporal variations of competition)

*Can also mimic immigration events when species becomes rare, which buffers species from extinction. This mechanism is not considered stabilising according to Chesson (2000b)

exclusion, especially at the sapling and mature stages. This is strengthened by the general decrease of density in the managed stand, which weakens intra- and interspecific interactions. Here also comes the recommendation of segregating species at the regeneration stage (Bauhus et al. 2016), which also slows down competitive exclusion and allows postponing interventions required to limit the most competitive species.

Other actions can promote stabilising mechanisms. Preferential selection of the most frequent species, whatever their identity, in the stand during tending or thinning operations (negative frequency-dependent selection; see “Example 3: frequency-dependent mortality”) can stabilise stand composition. This has been suggested by some authors as an efficient way to promote species richness in European forests (Wohlgemuth et al. 2002). By skipping parts of the maturing phase and the senescence stage, management also increases regeneration opportunities in low-disturbance-prone communities. Creating larger mean gap sizes can favour early successional species, triggering species coexistence through both successional and competition–colonisation trade-offs (see Example 1 above). Gap-based silviculture has been recommended especially when mid-tolerant or intolerant species are in competition with tolerant species (Coates and Burton 1997; Webster and Lorimer 2005). However, this approach might not be enough when highly competitive species are involved (i.e. the *Quercus petraea*–*Fagus sylvatica* example).

These examples of preferential selection for competitive species and gap-based silviculture are interesting because they represent two very different management practices that are difficult to combine and that potentially act preferentially on different coexistence mechanisms. The question of which to apply to maintain mixed stands can be considered in relation to the state of the mixture in the diagram of coexistence mechanisms (Fig. 1). When stabilising mechanisms are already strong (i.e. intraspecific competition is higher than interspecific competition) but not strong enough to maintain species mixing, then strengthening equalising mechanisms should be favoured. When stabilising mechanisms are weak, gap silviculture should

be favoured because it differentiates resources in space and time and thus can promote species coexistence provided species differ in their resource requirements, and gap characteristics are adapted to these requirements (Kern et al. 2017). When one species is competitively dominant and exploits the same resource as less competitive species, only regular planting interventions can help maintain the mixture.

5 How to move forward

Studies evaluating alternative strategies for forest management as well as studies relating biodiversity to the functioning of ecosystems traditionally have been based on three methodological pillars: (1) observational studies, (2) field experiments and (3) models. The problem is that so far, few studies have tried to analyse simultaneously the effects of species mixture and management on both species coexistence and the functioning of ecosystems. From our point of view, analysing mixing and management effects together is a necessary requirement if we want to develop a sound science of ecosystem management supporting both biodiversity and ecosystem functioning.

For observational studies, we need large permanent plots established under contrasted management regimes with a detailed monitoring of individual tree demography allowing for the estimation of population growth rates of each species and for the quantification of coexistence mechanisms. Then, we need experiments testing the effect of different management strategies (e.g. negative frequency-dependent selection of species, gap-based silviculture, planting non-competitive species, preferential selection of competitive species) on the maintenance of species mixture and ecosystem function. Most experiments examining the effect of species richness on ecosystem functions have been conducted on plantations and small plots that are relevant only to young development stages. We believe that experiments on adult stands where existing mixtures can be manipulated and different management options can be applied are powerful and underexplored options. Such

studies have been attempted in several places in North America (e.g. Sendak et al. 2003) and Europe (e.g. Seynave et al. 2018) but usually without trying to quantify the strength of coexistence mechanisms. Experiments testing different management options can also help to tease apart the possible coexistence mechanisms involved.

Finally, mechanistic individual-based models integrating climate effects, competition for resources and management appear to be crucial tools to provide a long-term perspective on forest dynamics under alternative management regimes (Rasche et al. 2011; Bauhus et al. 2016). Several studies (Bohn and Huth 2017; Morin et al. 2011) have shown the potential of such models to disentangle the ecological processes underlying the positive biodiversity effect on ecosystem function, while other models have concentrated on the effect of management actions or disturbance on the long-term maintenance of species mixing (Courbaud et al. 2015; Kunstler et al. 2013; Maily et al. 2000). Currently however, we are not aware of any modelling studies trying to link management, coexistence mechanisms and the functioning of ecosystems. New developments in the quantification of coexistence mechanisms (e.g. Ellner et al. 2016) could be inspiring for developing applications in such semi-mechanistic forest models. We believe that testing the interaction between management and biodiversity effects in these three approaches will help to make biodiversity research more functional for forest management.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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