



## Review

## The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process



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## ABSTRACT

Mixed-species forests and plantations sometimes have greater levels of ecosystem functions and services, including productivity, than monocultures. However, this is not always the case and there are many examples where mixtures are not more productive. Whether or not mixtures are more productive depends on the net effects of different types of interactions, and these are dynamic, changing through space and time. Many studies have examined how species interactions influence the growth of mixtures, but few have examined how spatial and temporal differences in resource availability or climatic conditions can influence these interactions. This review examines these spatial and temporal dynamics. The processes driving the dynamics are discussed using the production ecology equation, where plant growth is a function of resource availability, multiplied by the fraction of resources that are captured by the trees, multiplied by the efficiency with which the resources are used. Relative complementary effects depended on the types of species interactions and how resource availability changed. Complementary effects increased as soil nitrogen or water availability decreased when mixtures contained nitrogen fixing species, or when interactions were assumed to reduce competition for water. In contrast, some studies found that complementary effects increased with increasing site qualities, however in those studies there were no measurements of soil resource availability or any complementarity mechanisms. In those studies it was assumed that as growing conditions improved, competition for light increased and complementary effects resulted from interactions that improved light absorption or light-use efficiency. Multiple types of interactions can occur simultaneously in mixtures (e.g. nitrogen fixation, increased light absorption, and increased water-use efficiency) and so different resource availability-complementarity patterns will probably occur for a given pair of species, depending on the resource being examined. Less than half of the studies actually measured variables of the production ecology equation to indicate the processes driving the patterns. Several questions are listed that cannot yet be answered with confidence. Finally, stand structural characteristics, such as density, have also been shown to strongly increase or decrease complementarity effects and these need to be taken into account when interpreting results, but the mechanisms driving these density patterns were rarely quantified.

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## 1. Introduction

Many studies have shown that given the correct conditions, mixed-species forests and plantations can be more productive than monospecific stands (Assmann, 1970; Binkley, 1992; Kelty, 1992, 2006; Forrester et al., 2006b). However, interactions between a given pair of species are often dynamic, changing as resource availability or climatic conditions change, and it is not unusual for net complementary interactions between a given pair of species to transform into net competitive interactions, or vice versa (Binkley, 2003; Boyden et al., 2005; Pretzsch et al., 2010; Forrester et al., 2011; Bouillet et al., 2013). Understanding how these interactions change is necessary when managing mixtures and to determine what is driving productivity–diversity relationships, which are the net effects of many different species interactions. Understanding when and how species interactions will change is also critical given that one of the biggest current challenges in forestry is to adapt forest ecosystems to climate change. Mixed-species stands are viewed as one of the most important adaptation and risk-reduction strategies (Reif et al., 2010) so understanding how short-to long-term climatic variability can influence species interactions is considered a priority (Brooker, 2006).

The literature is reviewed to examine what is known about how complementary effects in mixed-species forests and plantations change spatially or temporally, and the importance of considering stand density when examining mixed-species interactions. The mechanisms that drive these patterns are examined using the production ecology equation (Eq. (1); Monteith, 1977).

$$\begin{aligned} \text{Gross primary production} &= \text{resource supply} \\ &\times \text{fraction of resource acquired} \\ &\times \text{resource use efficiency} \end{aligned} \quad (1)$$

Wood or above-ground biomass production can be examined using Eq. (1) after subtracting carbon allocation to respiration or non-woody tissues (Binkley et al., 2004). Several reviews have used this equation to understand the mechanisms driving growth responses to a wide range of factors, including geographic gradients, fertiliser application, irrigation, pruning, thinning, spacing, genotypes, species, stand age (Binkley, 2012; Forrester, 2013) and the influence of mixed-species interactions on plant nutrition (Richards et al., 2010).

Interactions between species growing in mixtures are often described in terms of competition, competitive reduction and facilitation (Vandermeer, 1989). Competition occurs when different plants or populations interact such that one exerts a negative effect on the growth or survival of the other. Competitive reduction occurs when inter-specific competition is less than intra-specific competition because of an inter-specific differentiation in resource use. Facilitation occurs when plants interact such that at least one species positively influences the growth or survival of another. The stress-gradient hypothesis (SGH) is often referred to when examining the dynamics of species interactions, and suggests that facilitation will increase, and competition decrease, as conditions become harsher (Bertness and Callaway, 1994). The SGH usually fits with observations in forests, however it is worth noting that it was largely developed outside of forest ecosystems, and definitions of facilitation usually differ between forest and SGH studies. In SGH studies facilitation is usually quantified by comparing the survival, growth or fitness of a plant growing with neighbours vs. without neighbours. This “without neighbours” situation is rare in forests, which have higher stand densities, and instead facilitation or competitive reduction are often assumed to have occurred when

growth (or survival) is greater with inter- than with intra-specific competition. Consistent with this contrast, a recent SGH meta-analysis and review by He et al. (2013) did not include any studies of tree–tree interactions unless the trees were in woodlands (not forests) or seedlings of tree species were examined.

## 2. Complementarity calculations and a conceptual complementarity model

Competitive reduction and facilitation often occur simultaneously and their effects can be difficult to separate, so in this review each of these are collectively described as complementarity. Many studies have examined the interactions that occur between trees in forests and these have been reviewed previously (Assmann, 1970; Binkley, 1992; Kelty, 1992, 2006; Forrester et al., 2006b; Richards et al., 2010), however far fewer studies have examined how these interactions are influenced by changes in resource availability and climatic conditions. These studies are summarised in Table 1 and are the focus of this review.

Figs. 1–6 contain complementary effects calculated using either tree or stand level data (Table 1). At the tree-level complementarity was calculated using the following equation:

$$\begin{aligned} \text{Complementary (\%)} &= \frac{\text{growth in mixture} - \text{growth in monoculture}}{\text{growth in monoculture}} \\ &\times 100 \end{aligned} \quad (2)$$

Eq. (2) is used for a tree of mean size in a stand of medium density (if a range of densities were examined). At the stand-level, complementarity was calculated using the following equation:

$$\begin{aligned} \text{Complementary (\%)} &= \left( \frac{\text{growth or yield in mixture}}{\text{growth or yield in monoculture} \times \text{species proportion}} - 1 \right) \\ &\times 100 \end{aligned} \quad (3)$$

In Eq. (3) the species proportion is the stand density of the given species in mixture/total stand density, and stand density is expressed as the initial planting density (trees ha<sup>−1</sup>) or current stand biomass. Eq. (3) will give a percentage that is exactly double the deviation from expected relative yield (yield of a species in mixture divided by its yield in monoculture) of a given species in mixture compared with its monoculture ( $\Delta RY_i$ ) that was used by Loreau and Hector (2001) to calculate the complementary and selection effects in mixed-species stands. However, in this review the complementary effects are at a species level, whereas in Loreau and Hector (2001) they were total stand effects. Total stand complementary effects are generally only mentioned in this review when the complementary effects were strong enough to result in transgressive over-yielding, where mixtures were more productive than monocultures of each species, this is indicated in Table 1. Over-yielding is not unusual in 2-species mixtures containing species with similar growth rates, but when there are large differences in growth rates, much larger complementary effects are needed for transgressive overyielding to occur, e.g. such as the potentially strong complementary effect of symbiotically fixed N on the growth of non-N-fixing trees (Forrester et al., 2006b).

Fig. 1 shows a conceptual model summarising the spatial and temporal dynamics of the complementarity effects in Figs. 2–6. The complementary effects will depend on (1) the types of species interactions (e.g. N-fixation, reduced competition for light), and (2) how resource availability changes along the spatial or temporal gradient. That is, complementarity should increase as the availability of a given resource declines, if the species interactions lead to

**Table 1**

Experiments that have examined the spatial or temporal dynamics of complementarity effects. When possible, these studies were used to produce Figs. 2–6. Studies examining temporal dynamics were only included when they also discussed the species interaction dynamics in relation to changing growing conditions (other studies are referred to in the text).

Study	Species	Climatic zone	How growing conditions changed	Resource influenced by species interactions during study period	Summary	Reference
1 <sup>a,b</sup>	<i>Alnus rubra</i> and <i>Pseudotsuga menziesii</i>	Temperate	N availability	Nitrogen	<i>P. menziesii</i> growth was improved in mixture at a low N site (due to N fixation by <i>A. rubra</i> ) but not at a high N site. Mixtures were more productive than <i>P. menziesii</i> monocultures at the low N site (transgressive overyielding) but not at the high N site. <i>A. rubra</i> contributed more to stand stem mass than <i>P. menziesii</i> at the high N site (until age 74 years) but at the low N site <i>A. rubra</i> contributed less than <i>P. menziesii</i> from about age 40 years and declined from about age 55 years	Binkley (2003)
2 <sup>b</sup>	<i>Pseudotsuga menziesii</i> and <i>Tsuga heterophylla</i>	Temperate, precipitation 2800–2902	Site quality	Light?	Mean tree <i>P. menziesii</i> growth was improved, compared with monocultures, at both sites. <i>T. heterophylla</i> growth was improved at the lower quality site but reduced at the higher quality site, because of intense competition from <i>P. menziesii</i> , which overtopped <i>T. heterophylla</i> . At the low quality site mixtures were more productive than <i>T. heterophylla</i> monocultures and similar (or more productive when mortality was considered – transgressive overyielding) to <i>P. menziesii</i> monocultures, but at the higher quality site, mixtures were less productive than <i>P. menziesii</i> monocultures	Amoroso and Turnblom (2006), Erickson et al. (2009)
3	<i>Picea glauca</i> x <i>engelmannii</i> , <i>Pinus contorta</i> , <i>Abies lasiocarpa</i> and <i>Populus tremuloides</i>	Sub-boreal, precipitation 440–900 mm	Site quality	Light?	The growth of <i>P. glauca</i> was strongly reduced by <i>P. contorta</i> neighbours on poor sites, but only weakly reduced on rich sites. Site quality did not change inter- and intra-specific competition coefficients for other species	Coates et al. (2013)
4	<i>Picea abies</i> and <i>Abies alba</i>	Temperate, precipitation 940–1850 mm	Site quality, climatic conditions	Light?	Absolute and relative complementarity increased for <i>A. alba</i> with increases in mean maximum temperature in August and mean minimum temperature in May, and for <i>P. abies</i> decreased with increasing mean maximum temperature in August but increased with mean minimum temperature in May and site index. The magnitude of these effects increased with increasing stand density	Forrester et al. (2013)
5 <sup>a</sup>	<i>Abies alba</i> with <i>Picea abies</i> and/or <i>Fagus sylvatica</i>	Temperate, precipitation 600–2000 mm	Water availability	Water	<i>A. alba</i> was less sensitive to summer droughts when in mixture than in monocultures, but only on dry sites. On wet or humid sites there was no complementary effect	Lebourgeois et al. (2013)
6 <sup>b</sup>	<i>Picea abies</i> and <i>Fagus sylvatica</i>	Temperate, precipitation 700–1270 mm	Site quality	All resources?	Transgressive overyielding occurred and was more likely at poorer sites. Complementary effects for <i>F. sylvatica</i> increased with increasing site quality because <i>P. abies</i> was a weaker competitor at those sites. As a result, <i>F. sylvatica</i> trees had higher crown projection areas for a given tree diameter in mixtures compared with monocultures, and this effect increased with increasing site quality. Complementary for <i>P. abies</i> increased as site quality declined, possibly due to facilitative effects of <i>F. sylvatica</i> on nutrient cycling	Pretzsch et al. (2010); Dieler and Pretzsch (2013)

Table 1 (continued)

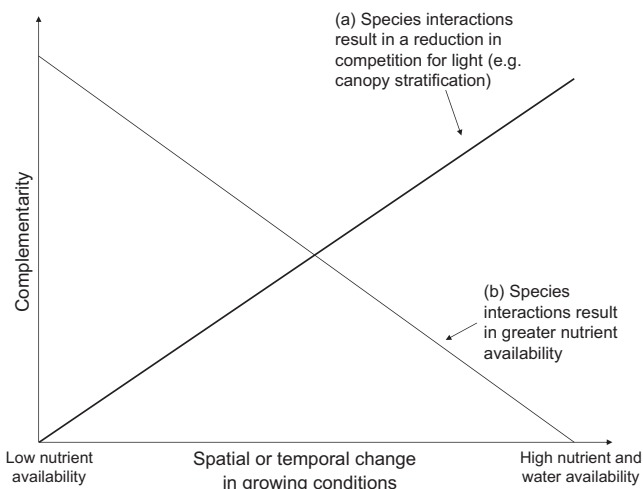
Study	Species	Climatic zone	How growing conditions changed	Resource influenced by species interactions during study period	Summary	Reference
7 <sup>b</sup>	<i>Fagus sylvatica</i> and either <i>Quercus petraea</i> or <i>Q. robur</i>	Temperate, precipitation 550–1120 mm	Site quality	All resources?	Complementarity effects for all species increased as site quality decreased, and there was transgressive overyielding on the low quality sites	Pretzsch et al. (2013b)
8	<i>Quercus petraea</i> , <i>Picea abies</i> and <i>Fagus sylvatica</i> ,	Temperate, precipitation 596–1343 mm	Site quality	Water or nutrients?	Complementary effects were observed during low-growth years but not during high-growth years. In mixtures, <i>F. sylvatica</i> was more resistant and resilient to droughts	Río et al. (in press), Pretzsch et al. (2013a)
9	30 European tree species	Temperate	Site quality	Light?	Stand productivity increased with species diversity, and the absolute complementarity effect increased with increasing site quality	Morin et al. (2011)
10 <sup>a,b</sup>	<i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i>	Temperate, precipitation 1000 mm	Site quality	Nitrogen	Growth of both species increased in mixtures and transgressive overyielding occurred. For <i>E. globulus</i> the complementary effect increased as site quality declined and as the stands aged, while the complementary effect for <i>A. mearnsii</i> declined as stands aged. Averaged across all stands mixtures were most productive because of N fixation by <i>A. mearnsii</i> , faster P cycling, increased APAR, water use, light-use efficiency, water-use efficiency and a shift in carbon allocation more to aboveground	Bauhus et al. (2004), Forrester et al. (2004, 2005, 2006a, 2007b, 2010b, 2011, 2012)
11 <sup>a,b</sup>	<i>Eucalyptus grandis</i> or <i>urophylla</i> x <i>grandis</i> and <i>Acacia mangium</i>	Tropical, 1130–1420 mm	Increasing N	Nitrogen	At the low N site (in the Congo) stem mass of both species was greater in mixture and transgressive overyielding occurred, but at the other sites (in Brazil), <i>Eucalyptus</i> were usually too competitive for <i>A. mangium</i> and mixtures were only more productive than <i>Eucalyptus</i> monocultures when they also had higher planting densities than <i>Eucalyptus</i> monocultures. Very intensive and long-term monitoring of these experiments indicated that in Brazil the superiority of the <i>Eucalyptus</i> over the <i>A. mangium</i> and competition for other resources (e.g. water) tended to outweigh facilitative effects of N fixation	Bouillet et al. (2008), Bouillet et al. (2013), Epron et al. (2013), Laclau et al. (2008), le Maire et al. (2013); Nouvellon et al. (2012)
12 <sup>a</sup>	<i>Eucalyptus saligna</i> and <i>Falcata</i> <i>mollucana</i> (syn. <i>Albizia falcata</i> )	Tropical, precipitation 1700–5000 mm	Water availability	Nitrogen	<i>E. saligna</i> growth was improved in mixtures, and at high rainfall sites this was due to N fixation, but at the low rainfall sites <i>F. mollucana</i> did not perform well and <i>E. saligna</i> grew better in mixtures due to a reduction in competition, not N fixation	DeBell et al. (1987)
13 <sup>a,b</sup>	<i>Eucalyptus saligna</i> and <i>Falcata</i> <i>mollucana</i>	Tropical, precipitation 4000 mm	N and P availability	N and P	<i>F. mollucana</i> growth increased in mixtures on low N soils but was outcompeted on high N soils. <i>E. saligna</i> growth was increased in mixtures on high P soils but not low P soils. These effects were modified by stand density. Transgressive overyielding occurred in the mixtures. Averaged across all stands, mixtures were more productive due to N fixation by <i>F. mollucana</i> , faster P cycling, increased APAR and increased light-use efficiency	Binkley (1992), Boyden et al. (2005), Binkley et al. (2003)

<sup>a</sup> These studies directly measured one or more variables of the production ecology equation. The others are useful for developing hypotheses about the patterns observed but provide limited information about the mechanisms driving the patterns.

<sup>b</sup> Had transgressive overyielding.

an increase in the availability, use, or use efficiency of that resource. These spatial and temporal changes in species interactions could occur at small to large scales. Spatially there is variability in light and soil resource availability at the scale of a few square

metres (Boyden et al., 2012), and climatic conditions can vary at small spatial scales due to canopy gaps, shading or wind protection from neighbours (Rao et al., 1998). At slightly larger spatial scales variability can occur along a slope and at different aspects, and of

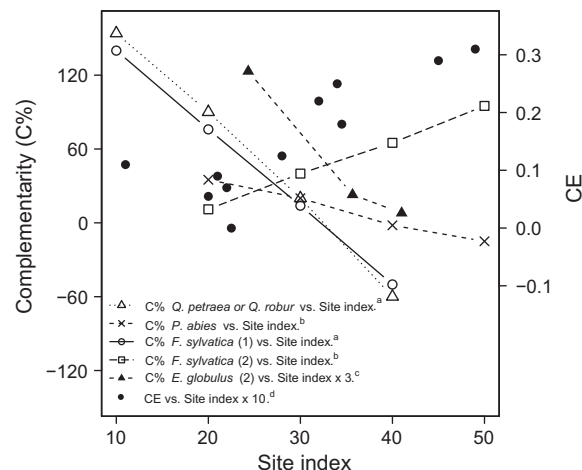


**Fig. 1.** A conceptual model showing the relative complementary response of a given species growing in a mixture, which depends on the gradient in growing conditions and the types of species interaction. The x-axis could show any gradient in growing conditions including changes in resource availability due to soil characteristics or competition, as well as from changes in climate that directly influence resource availability or indirectly influence availability by changing growth rates. Example (a) is where complementarity increases as competition for light becomes more intense because interactions increase light interception or light-use efficiency. When nutrients or water limit growth this type of interaction is less useful but as soil resource availability increases (or climatic conditions become more favourable) competition for light intensifies and any interaction that improves light interception or use efficiency will become more useful. Example (b) is where complementarity decreases as nutrient availability increases because the main interactions improve nutrient availability (e.g. accelerated rates of nutrient cycling) and will be more valuable when those nutrients are limiting. Modified from Forrester et al. (2013a).

course, there can be considerable variability at spatial scales of whole forests, plantations or regions. Similarly, species interactions could change due to temporal changes in climatic conditions ranging from short-term intra-annual climatic variability to long-term changes in climate. Temporal changes in species interactions also occur as stands develop, and demands for, and availability of, different resources vary.

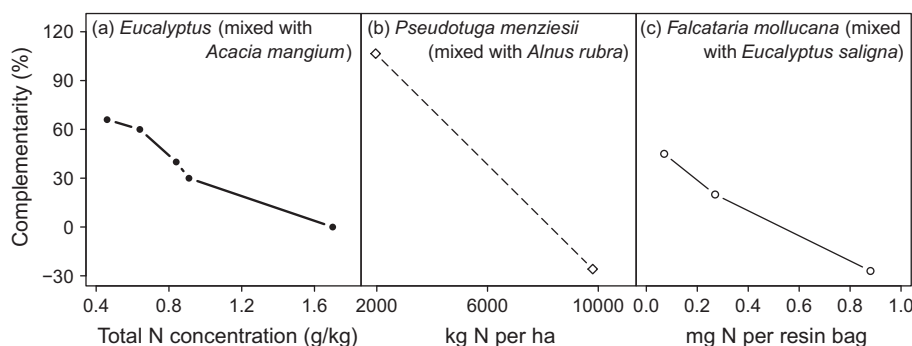
### 3. Spatial effects of interactions that influence nutrient availability

Mechanisms that improve nutrient availability, uptake and use efficiency often result in greater complementary effects on sites where that nutrient is limiting, consistent with the conceptual model of Fig. 1. Several examples of this trend are shown in



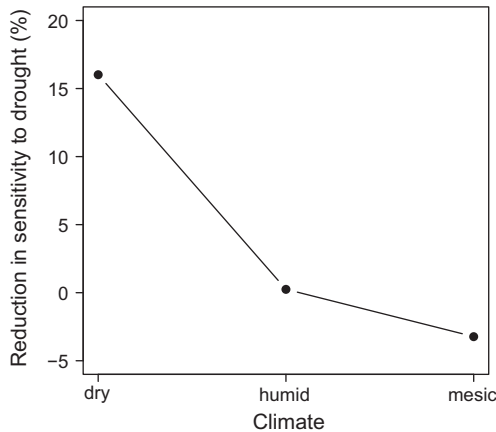
**Fig. 3.** The relationship between complementarity (C%) or complementarity effects (CE%), and site indices. C% was calculated using Eq. (3) and CE% is the complementarity effect of mixtures containing up to 30 species as calculated by Morin et al. (2011). Site index for C% studies is mean or maximum height at age 100 years, except for *E. globulus*, which was the monoculture volume ( $\text{m}^3 \text{ha}^{-1}$ ) at age 15 years, and site index for CE% is in  $\text{Mg ha}^{-1} \text{year}^{-1}$ . More information about each study is provided in Table 1. \*Study 7 (Pretzsch et al., 2013b), \*Study 6 (Pretzsch et al., 2010), \*Study 10 (Forrester et al., 2011), \*Study 9 (Morin et al., 2011) in Table 1.

Fig. 2. A classic example is the facilitative effect of nitrogen(N)-fixing species on the growth of non-N-fixing species, which increases as N becomes more limiting (Binkley, 2003; Forrester et al., 2006b,c; Bouillet et al., 2013). For example strong facilitative effects of the N-fixing *Alnus rubra* on the growth of *Pseudotsuga menziesii* were found on a site with low soil N, but not on a site with high soil N (Study 1, Binkley, 2003). Following the production ecology equation, this site effect was related to increases in nutrient uptake rather than changes in availability or efficiencies. Even though uptake rates, especially N, Mg and K, were greater in mixtures than in *P. menziesii* stands at both sites, the relative increases were much greater at the low N site (Binkley et al., 1992b). In contrast, rates of N fixation by *A. rubra* were high at both sites, and the accumulation of N in mixtures compared with *P. menziesii* stands was also high at both sites (Binkley et al., 1992b). N-use efficiencies in mixtures were only 25% and 16% of those in *P. menziesii* stands on low and high N sites, respectively (Binkley et al., 1992b). Increases in nutrient availability can lead to a reduction in the proportion of carbon that is allocated below-ground because fewer roots are required to capture soil resources and the carbon can then be used above-ground to capture more light and fix more carbon (Litton et al., 2007; Poorter et al., 2012). Biomass or carbon partitioning were not measured in these *A. rubra* – *P. menziesii*

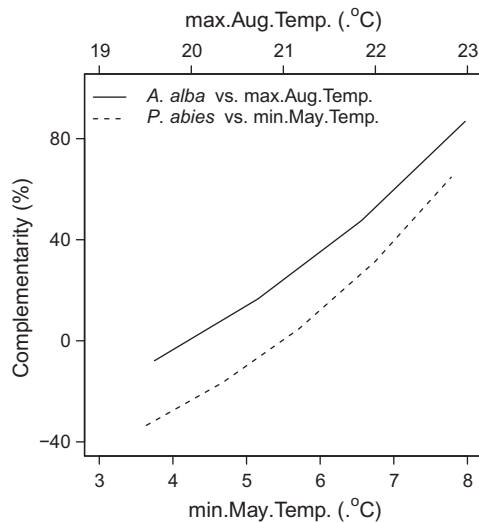


**Fig. 2.** The relationship between complementarity (%), calculated using Eqs. (2) and (3), and N availability, for (a) *Eucalyptus* (Study 11; Bouillet et al., 2013), (b) *Pseudotsuga menziesii* (Study 1; Binkley, 2003), and (c) *Falcata mollucana* (Study 13; Boyden et al., 2005). More information about each study is provided in Table 1.





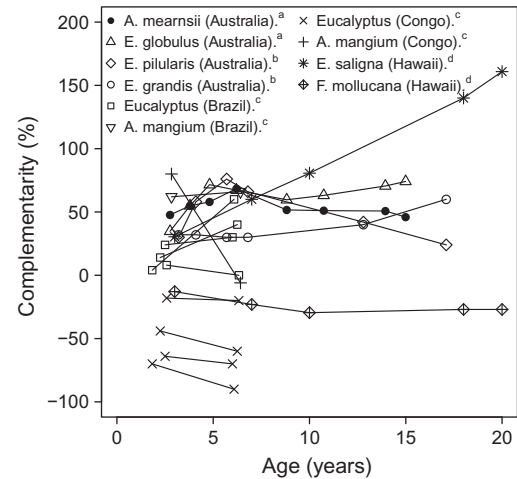
**Fig. 4.** The relationship between the relative reduction in drought sensitivity (%) of *A. alba* (in mixtures with *P. abies*) and climate, from Study 5 in Table 1 (Lebourgeois et al., 2013). The reduction in sensitivity is the mean sensitivity (as calculated by Lebourgeois et al., 2013) of trees in mixtures compared with monocultures relative to the sensitivity of monocultures.



**Fig. 5.** The relationship between complementarity (%), calculated using Eq. (2), and mean maximum temperature in August or mean minimum temperature in May (which varied between sites) in mixed *A. alba* and *P. abies* forests (Study 4 in Table 1).

stands, but two studies of mixtures that contained N-fixing *Acacia* trees with *Eucalyptus* trees found that when mixtures were more productive than monocultures, the proportion of carbon allocated above ground was more than 20% greater than that of *Eucalyptus* monocultures (Forrester et al., 2006a; Epron et al., 2013), so part of the improved above-ground growth was due to a reduction in the proportion of carbon partitioned below ground. Other examples of increasing facilitative effects with decreasing soil N are shown in Fig. 2 and Table 1. These studies show that when resources other than those that are influenced by species interactions (e.g. N) are the main limiting resources, then competition for the former can outweigh any facilitation effects and there are many cases where productivity was not improved in mixtures containing N-fixing species because N was not limiting enough and/or the N-fixing species were outcompeted by the non-N-fixing species for other resources (Fig. 2, Forrester et al., 2006c; Bouillet et al., 2013; Epron et al., 2013).

The trends shown in Fig. 2, which result from natural gradients in nutrient availability, could potentially be used by managers to



**Fig. 6.** Temporal dynamics of complementary effects in 1:1 mixtures of *Eucalyptus* sp. with other *Eucalyptus* sp. or with N-fixing species. <sup>a</sup>Study 10 (Forrester et al., 2011), <sup>b</sup>(Forrester and Smith, 2012), <sup>c</sup>Study 11 (Bouillet et al., 2013), <sup>d</sup>Study 13 (Binkley et al., 2003) in Table 1.

manually increase facilitative effects. This could be done by increasing the availability of other resources, which are not significantly influenced by species interactions, but that are also limiting growth. For example, the facilitative effects of N-fixing species on eucalypts increases along natural gradients of phosphorus availability and can be increased by applying phosphorus fertiliser (Boyden et al., 2005; Forrester et al., 2006c).

It is important to note that high site quality is not necessarily a good indicator that responses to N additions will be small. Even on relatively productive sites, as long as N is a growth-limiting resource, significant increases in productivity can be gained by admixing N-fixing species (e.g. Study 13, DeBell et al., 1987; Binkley et al., 2003). In a review of the facilitative effects of N-fixers in eucalypt plantations, some of the largest facilitative effects were found in some of the most productive plantations (Forrester et al., 2006b), and there was no significant relationship between the mean annual biomass or volume growth of eucalypt monocultures (a measure of site quality) and the relative yield in 1:1 mixtures. This shows the risk of relying on site quality or site indices when studying how plant interactions change.

Instead of increasing nutrient pool sizes, e.g. N fixation, the proportion of the total soil nutrient pool that is actually available to plants can be increased. This may result from accelerating rates of nutrient cycling, contrasting mycorrhizal associations, or contrasting fine-root distributions (Rothe and Binkley, 2001; Richards et al., 2010; Hinsinger et al., 2011). Of these mechanisms, nutrient cycling has received the most attention in mixed-species forests and a review of this process found that linear effects are the most common, such that values in mixtures are intermediate between monocultures, but complementary and negative effects also occur (Rothe and Binkley, 2001). Any mechanism that improves nutrient availability should be more useful on sites where the given nutrient is limiting growth (see Fig. 1). Increasing complementary effects with decreasing site quality were found for *P. abies* mixed with *F. sylvatica* (Study 6, Pretzsch et al., 2010), and for each species in mixtures of *Fagus sylvatica* with either *Quercus patraea* or *Q. robur* (Study 7, Pretzsch et al., 2013b) (Fig. 3). This pattern was suggested to have resulted, at least partly, due to traits or species interactions that reduced competition for, or improved the availability of, nutrients, although nutrient availability and nutrient uptake were not actually measured along the gradients. Similar trends were suggested for *Picea mariana* and *Populus tremuloides*

mixtures (Cavard et al., 2011). There is no strong evidence, however, that such improvements in nutrient cycling alone (as opposed to N fixation) are large enough to result in transgressive over-yielding. Nevertheless this might be possible if a fast nutrient cycling species was matched with a more resource (light, water or nutrient)-use efficient species, and Rothe and Binkley (2001) suggested that improvements in nutrition are most likely when a deeper rooting species that exploits nutrient-rich subsoil layers acts as a “nutrient pump” for more shallow rooted species.

#### 4. Spatial effects of interactions that influence water availability

Following the model in Fig. 1, interactions or mechanisms that influence water availability and uptake will be more useful where water is limiting (Fig. 4). For example, *Abies alba* was found to be less sensitive to summer droughts when growing in mixtures with *Picea abies* or *Fagus sylvatica* than when growing in monospecific neighbourhoods and this complementary effect was only found at dry sites and not at mesic or humid sites (Fig. 4, Study 5, Lebourgeois et al., 2013). It was suggested that competition for water was reduced for *Abies alba* because the other species have shallower roots systems, thereby reducing competition for deeper soil water, and they also have lower canopy interception. Hydraulic redistribution, whereby roots acquire water from moist soil and release it into upper and drier soil layers (Neumann and Cardon, 2012), has also been suggested as a possible mechanism leading to greater complementary effects with decreasing site quality in *F. sylvatica* and *Q. petraea* mixtures (Study 7, Pretzsch et al., 2013b). However, water availability, uptake or use efficiencies were not measured in that study, and interestingly, another study using the same species found that while *Q. petraea* redistributed water from deeper to more shallow regions of the soil, there was no evidence that *F. sylvatica* actually used that water (Zapater et al., 2011). The contribution of this mechanism to the overall observed complementary effects in mixed-species forests does not appear to have been quantified along gradients in water availability. Nevertheless, at a single-site study, where mixtures were more productive than monocultures, the mixtures also used more water and used it more efficiently than monocultures of all component species, even during a drought period (Forrester et al., 2010b). Complementarity involving improved water relations may not necessarily only occur at dry sites, but also at sites that experience seasonal water deficits or periodic droughts (see below). These studies and the trend shown in Fig. 4, indicate that an important question for future research is how do differences in water use and water-use efficiencies between monocultures and mixtures (of a given species combination) change along gradients in water availability, and how much can be attributed to mechanisms such as hydraulic redistribution, or spatial and temporal differences in the ways different species obtain water and influence water availability?

#### 5. Spatial effects of interactions that influence light absorption and use

Increasing complementary effects with increasing site quality, or as climatic conditions improve, have been observed in several studies (Figs. 3 and 5). While none of those studies quantified the mechanisms behind the response by measuring the variables on the right-hand side of the production ecology equation, they are useful for developing hypotheses that can be tested in new experiments. For example, one of those (Study 6) showed that for a given tree diameter, the crown projection area of *F. sylvatica* trees was larger in mixtures than in monocultures, and this effect increased with site quality (Dieler and Pretzsch, 2013). Increased crown size might have improved light interception. As availability

of water and nutrients increase, stand leaf area and absorbed photosynthetically active radiation (APAR) increase, while competition for light increases and trees respond by allocating a higher proportion of their growth above ground to facilitate light absorption (Litton et al., 2007; Poorter et al., 2012). Under these circumstances, and following the conceptual model in Fig. 1, interactions that improve APAR and light-use efficiency (LUE) may increase in importance with increasing soil resource availability, or more favourable climatic conditions, thereby increasing complementary effects as shown in Figs. 3 and 5 (Kelty, 1992). It is worth noting that increasing complementarity with improving soil resource or climatic conditions may appear to be inconsistent with the SGH, but it is consistent when competition for light is considered to be the stressor. Thus all the studies in this review could be considered to fit with the SGH even though some of the complementarity interactions are competitive reduction (not facilitation as in the SGH) and the calculation of complementarity using Equations 2 and 3 is not the same as the calculation that is typically used in SGH studies (no neighbours vs neighbours), as explained in the Introduction.

There are several ways APAR or LUE could be increased in mixtures. The combination of a species with high growth rates and high LUE that overtops a slower-growing and more shade tolerant species could have a greater LUE than monocultures of the more shade tolerant species and may be capable of higher APAR than monocultures of the less shade tolerant upper canopy species. No studies could be found that measured APAR or LUE of each species in mixtures along resource availability gradients; however a few studies have examined light at single sites. *Eucalyptus saligna*-*Falcata* mixtures and *Eucalyptus globulus*-*Acacia mearnsii* mixtures each had greater APAR and LUE than monocultures of either species (Binkley et al., 1992; Forrester et al., 2012). In both cases the eucalypts were more light-use efficient, but their growth was limited by N. *F. mollucana* and *A. mearnsii* are N-fixing species but they are not as light-use efficient as the eucalypts. The mixtures combine the high LUE of the eucalypts with the higher N availability under the N fixers. Also, since the LUE of the mixtures was greater than that of both monocultures, rather than a weighted average, the LUE of at least one of the species must have increased in mixture compared with its monoculture. This is consistent with a literature review that showed that, for a given species, LUE often increases (but does not decrease) as growth increases (Binkley, 2012). In addition, the eucalypts overtopped the N-fixing species, so until the eucalypt canopy closes above the N-fixing species there should be more space between the eucalypt crowns in mixtures than in monocultures, and the eucalypts should not be shaded as much from the sides as eucalypt trees in monocultures. Therefore, light availability and APAR per eucalypt tree may also have been greater in mixture compared with eucalypt monocultures. In more extreme cases APAR per tree could increase for one species at the expense of the other because the former is better suited to the site and out-competes the latter. For example, in 1:1 *E. grandis* and *A. mangium* mixtures the eucalypts overtopped the acacia and stand APAR was higher than that of monocultures of either species (le Maire et al., 2013), similar to the studies above. However, the growth of mixtures was intermediate between faster growing *E. grandis* monocultures and slower growing *A. mangium* monocultures because the LUE of both species was lower in mixtures, and because even though mean tree *E. grandis* growth and APAR increased compared with trees in monocultures, this was at the expense of lower mean tree *A. mangium* growth and APAR in the mixtures.

An interesting question for future work is why are there positive relationships between complementarity and site quality (Fig. 3) or the climatic variables that improved growth in Fig. 5? When APAR and/or LUE are higher in mixtures, do these

differences become greater, thereby increasing complementary effects, as soil resource availability increases or as climatic conditions improve? This applies at the stand, the individual tree and the species levels.

## 6. Temporal effects and interactions between resources

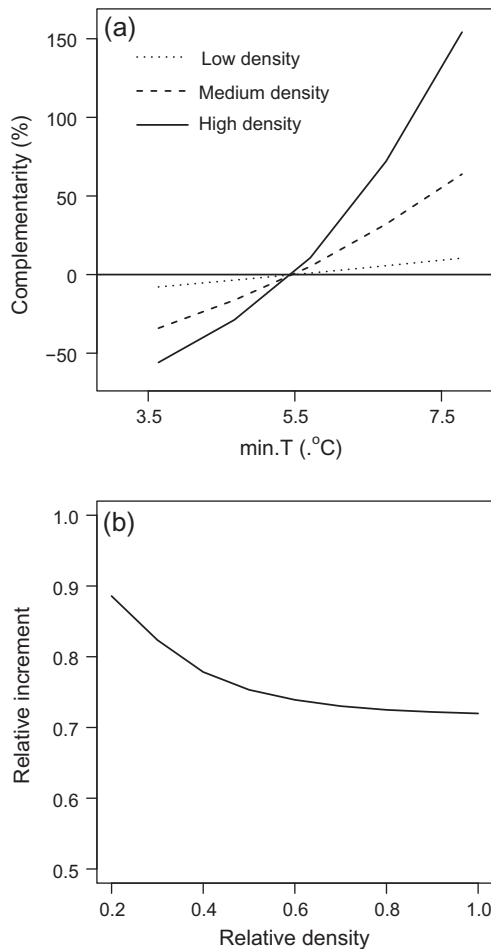
Temporal changes in species interactions result from abiotic factors, such as climatic conditions and stand disturbances, or stands developing and potentially influencing the availability of light and soil resources. Considering all of these factors, and the fact that different species often have contrasting growth dynamics, it is not surprising that as stands develop there are often changes in the relative dominance of species or complementarity effects, in terms of the relative growth of mixtures compared to monocultures (Fig. 6) (Burdon and Chilvers, 1974; Duff et al., 1983; Larson, 1986; Noble, 1989; Binkley, 2003; Filipescu and Comeau, 2007; Cavard et al., 2011; Forrester et al., 2011; Bouillet et al., 2013). This also implies that information about mixture effects during a single point in time may not be a good reflection of actual long-term mixture effects. For example, the magnitude of complementarity effects could vary with the intensity of competition for light. As stands develop and the canopy closes, competition for light increases and light can become a major growth limiting resource. In response, trees can allocate a higher proportion of growth aboveground as stands develop (Litton et al., 2007), which should facilitate light capture. It will then be important for shade intolerant species to overtop more shade tolerant species (Kelty, 1992). Eucalypt species are notoriously shade intolerant and when planted in mixtures complementary effects are more likely when the eucalypts are able to overtop more shade tolerant species, even if this canopy stratification takes several years to develop (Study 10, Forrester et al., 2006b, 2011). Similarly, temporal changes in the magnitude of complementarity can depend on competition for water. As even-aged stands develop, stand leaf areas and growth rates initially increase before peaking and then declining (Ryan et al., 1997). Transpiration rates can follow a similar trend (Dunn and Connor, 1993; Vertessy et al., 1996; Forrester et al., 2010a). In addition to these age-related changes, transpiration may increase further when mixtures are more productive than monocultures (Forrester et al., 2010b; Kunert et al., 2012). As transpiration rates increase towards the peak, soil water availability may decline and stands may become water limited and more susceptible to hot or dry periods. This susceptibility may be even greater, and occur earlier, in mixed species stands when they are more productive than monocultures. This was reported in several stands where early complementary effects were observed in mixtures only to be lost later due to excessive competition for water (Snowdon et al., 2003; Forrester et al., 2007a; Bouillet et al., 2013). In these mixtures the complementarity effects resulted largely from improved N availability due to N-fixing species. In contrast, interactions and traits that reduce competition for water may ameliorate this effect and reduce the sensitivity of trees to hot and dry periods, and this effect should be more useful during periods of actual water stress. Dendrochronology studies have also examined temporal variability in species interactions by using growth indices of trees in mixtures and monocultures during low- and high-growth years. In mixtures of *Quercus petraea*, *Picea abies* and *Fagus sylvatica*, complementary effects were observed during low-growth years but not during high-growth years (Study 8, Río et al., in press) and *F. sylvatica* was more resistant and resilient to droughts when in mixture (Study 8, Pretzsch et al., 2013a). Consistent with Fig. 1, the authors speculated that complementary effects resulted from improved water relations, although no direct measures of water availability or water stress were examined (e.g.

soil moisture availability or physiological parameters), so the magnitude and presence of differences in water stress between mixtures and monocultures were unknown.

## 7. Stand structure

Stand density may also influence species interactions and growth in mixed-species forests. Stand density is important for at least two reasons when analysing species interactions. Firstly, stand growth usually increases with density initially before levelling off at higher densities, and stand density can be positively correlated with species diversity (e.g. Chisholm et al., 2013; Vilà et al., 2013). Therefore greater productivity in mixtures may sometimes result from higher densities or greater structural diversity more than from direct effects of species diversity or species interactions *per se* and so stand structure, at least in terms of stand density, needs to be controlled, or accounted for, to avoid over- or underestimating complementarity effects. The effects of inter- and intra-specific interactions and stand density can be separated at the tree level using competition indices (Boyden et al., 2005; Vanclay, 2006; Forrester et al., 2013a), or at the stand level using designs such as replacement and additive series (Kelty and Cameron, 1995) or by thinning mixed species forests to create monocultures and plots with the same starting densities. The second reason why density is important is because the complementary effects described above can all be influenced by stand density. At very high densities competition may outweigh complementary effects. For example, many studies have shown facilitative effects of *Acacia* in *Eucalyptus* plantations, but when the *Acacia* are weeds, which may involve very high densities, e.g. 1300–20,000 *Acacia* trees per ha in addition to about 1000 *Eucalyptus* trees per ha, there are net competitive effects on *Eucalyptus* growth, even though soil nitrogen increases with *Acacia* density (Hunt et al., 1999). In contrast, at low densities most interactions will be weak, regardless of whether they are complementary or competitive, and the relative and absolute complementary effects should initially increase with increasing density simply because the plants have to be close enough to interact for there to be any complementarity. Between these extremes, the relationship between density and complementary effects will depend on the resources that are limiting (i.e. that are influenced by changes in density) as well as the types of species interactions. Increasing stand density has been shown to both increase and reduce complementary effects in mixed-species forests or plantations (Fig. 7) (Garber and Maguire, 2004). Increasing stand density, quantified using competition indices, increased complementarity in *P. abies* and *A. alba* mixtures on sites where mixtures were more productive than monocultures, but increased competitive effects on sites where mixtures were less productive than monocultures (Study 4, Fig. 7, Forrester et al., 2013a). Increasing stand density also increased complementarity effects in mixtures where *Pseudotsuga menziesii* overtopped *Tsuga heterophylla* (Amoroso and Turnbull, 2006). In mixtures of *Pinus sylvestris* and *F. sylvatica*, complementary effects increased with increasing density for *F. sylvatica* but declined for *P. sylvestris* (Condés et al., 2013). *F. sylvatica* is a strong competitor and grows better in mixtures because *P. sylvestris* is a weaker competitor. This effect becomes more pronounced as stand density increases. In contrast, at high densities, any facilitative effects that *F. sylvatica* could have on *P. sylvestris* are outweighed by the intense competition and so complementarity effects for *P. sylvestris* are greater at lower densities (Condés et al., 2013). Complementary effects were also higher at lower densities for both species in *Pinus sylvestris* and *Quercus pyrenaica* mixtures (Fig. 7, Río and Sterba, 2009). Increasing stand density, quantified using competition indices, increased or decreased complementary effects for *Falcataria mollucana* and





**Fig. 7.** The effect of stand density on complementary effects. (a) Shows increasing complementary effects for *P. abies* in mixtures with *A. alba* as stand density increases (modified from Forrester et al., 2013a). The complementary effect is plotted against a site gradient in mean minimum temperature in May (min.T). (b) Shows decreasing complementary effects (in terms of relative increment) for *Pinus sylvestris* in mixture with *Quercus pyrenaica* as stand density increases (modified from Río and Sterba, 2009). Relative density is the basal area per ha of *P. sylvestris* in monoculture divided by the maximum observed basal area per ha of *P. sylvestris* stands. Relative increment is the increment ( $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ ) of *P. sylvestris* in mixture divided by its increment in monoculture.

*Eucalyptus saligna*, depending on how soil N and P availability changed (Study 13, Boyden et al., 2005). These studies clearly show that stand density modifies species interactions, and this will also have implications for the effects that thinning could have on species interactions when it is not accounted for and varies between mixtures and monocultures. However, the mechanisms behind the contrasting effects are not well explained because few studies quantify resource availability, such as in Study 13, or resource uptake and use efficiency.

## 8. Conclusions and implications for future research

The literature reviewed above indicates that for a given species combination, there are probably several different processes that lead to the net complementary (or competitive) effects. For example in mixtures that contain N-fixing species, there are also processes that reduce competition for light and accelerate rates of P cycling (Binkley et al., 1992a; Forrester et al., 2005; Richards et al., 2010; Hinsinger et al., 2011). The contribution of these processes to the net complementary effects will change with spatial and temporal variability in resource availability or

climatic conditions. That is, a given species combination may show several resource availability – complementarity patterns depending on the temporal or spatial gradients being examined. For example, complementary effects in *Abies alba* and *Picea abies* forests increased as site productivity or temperature increased (Fig. 5) (Study 4, Forrester et al., 2013a). This analysis was based on average climatic conditions. In contrast, for the same species combination, but when growth sensitivity was examined focusing on low-growth years, complementary interactions were greater at dry sites than humid or mesic sites (Fig. 4), probably due to reductions in competition for water (Study 5, Lebourgeois et al., 2013). In isolation each of these studies will underestimate the value of the complementarity. Similarly, asymptotic productivity-biodiversity relationships (Vilà et al., 2013) might suggest that some species are redundant in more diverse stands. However, studies in grassland mixtures have shown that when more functions (productivity, nutrient cycling, pest protection, etc.) and more growing conditions are considered (ages, environmental conditions) the number of species required to reach an asymptote increases because there is a greater chance that each will be useful under specific conditions (Hector and Bagchi, 2007; Isbell et al., 2011). Similarly, the absence of productivity-biodiversity relationships in some forests (Vilà et al., 2013) may result from combinations of species that do not interact in ways that improve the availability or use of the limiting resources during the measurement period. For example, when water limits growth, having a wide range of nutrient uptake strategies may be of little benefit.

Several studies in Table 1 and Fig. 3 show patterns where complementary effects change with site quality, and these are useful for developing hypotheses, but they provide limited information about the causes of these patterns. Site quality or site indices are often used but are problematic because they are the net effects of many different climatic and soil factors so it is difficult to determine which factors were actually responsible for the observed patterns, or whether different factors were responsible under different conditions. This is important because it is these factors that influence the species interactions, not the productivity (site index) of the site *per se*. Progress in understanding the growth dynamics of mixed-species forests will benefit if the processes driving the patterns are quantified and the conditions that strongly influence those processes are also quantified (see also Rothe and Binkley, 2001). This could be done using carefully designed planted experiments on uniform sites and by measuring growth, resource availability, uptake and efficiency, and biomass partitioning. Alternatively, quicker results could be obtained by making use of existing mixed-species forests on a broad range of sites and using thinning to control initial stand density and to create single-species plots.

Lastly, four questions are listed below that cannot currently be confidently answered and that will require well designed, geographically distributed experiments.

1. How do differences in water use and water-use efficiencies between monocultures and mixtures change along spatial or temporal gradients in water availability, and how much do different mechanisms contribute to these effects (e.g. hydraulic redistribution, interspecific differences in uptake or WUE or canopy interception, etc.).
2. When APAR and/or LUE are higher in mixtures, do these differences become greater, thereby increasing complementary effects, as soil resource availability increases?
3. How much does faster nutrient cycling (in mixtures without N-fixing species) increase the resource uptake and resource-use efficiency of the mixtures, and does this result in significant complementary effects and even transgressive over-yielding?

4. Why does stand density influence complementarity effects, in terms of the variables of the production ecology equation, and how do different types of species interactions influence these trends?

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