In seasonal tropical forests, evergreen–deciduous mixtures are more productive than monocultures because they intercept more light throughout the year, reflecting complementary resource use by functional groups possessing different traits. This suggests that temperate and boreal forests may also exhibit overyielding, due to the difference in phenology between gymnosperms and angiosperms. However, complementarity could also arise from differences in morphology between needle leaves and broad leaves, or facilitation by N-fixing species. Alternatively, mixtures may be more productive simply because interspecific competition is less intense than intraspecific competition. We used forest inventory data to assess the complementarity of the main functional groups in Switzerland. We employed a trait-based analysis of competition to determine whether: 1) trait differences reduce the intensity of competition between complementary functional groups, 2) complementarity is observed along a broad altitudinal temperature gradient. N-fixing species facilitated the growth of non-fixing species, such that 50/50 mixtures were 50% more productive than monocultures, though half the overyielding was due to the alleviation of intraspecific competition. In contrast, we found no evidence of complementarity between evergreen and deciduous species. For example, in stands where larch was mixed with other gymnosperms, there was no reduction in heterospecific competition among evergreen species, even though evergreens cast shade on one another throughout the year. In cold montane forests, broadleaf species reduced the suppression of needleleaf species, and vice versa. Thus, 50/50 mixtures of needleleaf and broadleaf species were 15% more productive than needleleaf monocultures. However, in warm lowland forests, broadleaf species exacerbated the suppression of needleleaf species, completely offsetting the positive effect that needleleaf species had on broadleaf species. In summary, we found no evidence of complementarity between evergreen and deciduous species, but needleleaf–broadleaf mixtures exhibited overyielding in cold montane forests, which is consistent with the stress gradient hypothesis, though the underlying mechanisms remain uncertain.

Keywords: competition, leaf traits, mixed forests, overyielding, plant–plant interactions, stress gradient hypothesis
Introduction

Biodiversity–productivity experiments have shown that species mixtures containing multiple functional groups are more productive than species mixtures containing only one functional group, even if the number of species is held constant across all treatments (Reich et al. 2004, Mouillot et al. 2011). The enhanced productivity of these mixtures is called overyielding, and is the result of complementary resource use by functional groups that possess different traits. For example, biodiversity–productivity experiments conducted in seasonal tropical forests have also documented overyielding in mixtures of evergreen and deciduous tree species, indicating that these two functional groups exhibit temporal niche complementarity due to their difference in phenology (Sapijanskas et al. 2014). In particular, species differences in phenology allow mixtures to intercept more light throughout the year than stands comprised of only one of the functional groups (Forrester and Pretzsch 2015, Forrester and Bauhus 2016), a phenomenon known as temporal light partitioning.

This suggests that overyielding may also occur in temperate and boreal forests (Cannell et al. 1992, Scherer-Lorenzen et al. 2005), due to the difference in phenology between gymnosperms and angiosperms (Ishii and Asano 2010, Lu et al. 2016), provided that the shoulder growing seasons for evergreen species (before emergence and after abscission of deciduous leaves) are long enough to allow for temporal niche complementarity (Chabot and Hicks 1982, Kikuzawa 1991, Givnish 2002, van Ommen Kloeke et al. 2012). Yet, complementarity could arise from other trait differences between these two functional groups, such as the difference in morphology between needle leaves and broad leaves (Augusto et al. 2015). For example, leaf litter quality has a profound influence on decomposition and nutrient cycling (Cornwell et al. 2008), so mixing these very different litters may allow for complementary use of soil resources by needleleaf and broadleaf species (Gessner et al. 2010).

Numerous studies have examined the productivity of monocultures and mixed stands comprised of two common temperate species such as Norway spruce and European beech (Pretzsch 2005, Pretzsch et al. 2017). However, such pairwise replacement studies generally do not attempt to disentangle the effects of phenology and leaf morphology. Nevertheless, they do have considerable practical value because conifer stands are being widely converted to mixed stands that include a variety of species (Knöke et al. 2008). Thus, the results of pairwise replacement studies must be generalized by assessing complementarity across a broad variety of species and functional groups (Mina et al. 2017), including mixtures of evergreen and deciduous gymnosperms, in order to assess the complementarity of species differing in phenology separately from that of species differing in leaf morphology. Furthermore, complementarity must be assessed across a broad range of climates, in order to determine whether overyielding increases as temperature decreases (Paquette and Messier 2011, Potter and Woodall 2014, Wu et al. 2015, Jucker et al. 2016, Mina et al. 2017), as predicted by the stress gradient hypothesis (Bertness and Callaway 1994, Jucker et al. 2016).

In this paper, we use forest inventory data to examine the wealth of species interactions observed in pre-existing plots spanning a large altitudinal temperature gradient in Switzerland (Brändli et al. 2010). We conducted a trait-based analysis of competition to assess the complementarity of the main functional groups, including a deciduous gymnosperm (for the reason given above) as well as three N-fixing angiosperms, in order to demonstrate the utility of our trait-based methods using a functional group (N-fixing angiosperms) that is known to promote overyielding through facilitation. However, since overyielding also occurs in the absence of facilitation, our method focuses on competition as a common mode of interaction between complementary species.

Our analysis builds on the method developed by Kunstler et al. (2016), which was designed to quantify how trait differences reduce the intensity of competition between two or more complementary species, thereby promoting overyielding. In contrast, many biodiversity–productivity studies do not directly assess the impact of one species on another, because they do not explicitly quantify the intensity of competition, or how it varies with trait differences. We modified the method of Kunstler et al. (2016) to estimate a set of ‘pairwise dissimilarity effects’ that quantify how binary trait differences affect the intensity of competition between complementary functional groups (as opposed to species), while allowing for asymmetric interactions in which only one species benefits from the interaction.

Our study was designed to address the following questions regarding mixtures that contain two or more functional groups: 1) Do differences in phenology reduce the intensity of competition between evergreen and deciduous gymnosperms? 2) Do differences in phenology or leaf morphology reduce the intensity of competition between angiosperms and gymnosperms? 3) Do N-fixing species facilitate the growth of non-fixing species, indicating that the supply of extra nitrogen completely offsets any competitive effects? 4) Do these dissimilarity effects cause overyielding in any of the following mixtures: evergreen and deciduous gymnosperms, needleleaf gymnosperms and broadleaf angiosperms, N-fixing and non-fixing angiosperms? 5) Do these dissimilarity effects depend on temperature, such that the magnitude of overyielding varies across the altitudinal temperature gradient?

Material and methods

We used data from the National Forest Inventory (NFI) of Switzerland, which is inventoried on a 1 × 1 km grid covering the entire country (Brassel and Lischke 2001). The inventory plots span a broad gradient in altitude, from 281 m a.s.l. in the lowlands to 2218 m a.s.l. in the Alps, and a broad gradient in mean annual temperature, from 12.2°C to 0.6°C, respectively (Supplementary material Appendix 1). Montane forests with mor soils are dominated by gymnosperms (e.g. spruce, fir and larch), whereas lowland forests with mul
soils are dominated by angiosperms (e.g. beech, maple and ash). However, both groups co-occur across the gradient, and angiosperms are locally abundant in montane forests, particularly in young stands on recently disturbed sites, while gymnosperms are locally abundant in lowland forests, particularly in managed stands. In these cases, local abundance reflects transient dynamics driven by natural disturbance and/or management.

Data collection

We used data from the first and second census (1983-1995), and excluded plots that were harvested between the two census periods. The resulting dataset included 2891 plots consisting of two concentric circles with the following horizontal projection area: a 200 m² plot for sampling trees 12-36 cm DBH, and a 500 m² plot for sampling trees \( \geq 36 \) cm DBH. The diameter and species identity of each tree was measured in both censuses, except trees which died or were cut by the second census, in which case the status of the tree was recorded. The dataset includes 50 species from 4 functional groups possessing a different combination of 3 binary traits: needleleaf/broadleaf, evergreen/deciduous, N-fixer/non-fixer (Supplementary material Appendix 1). The functional groups include evergreen gymnosperms, deciduous gymnosperms, deciduous angiosperms, and N-fixing angiosperms (also deciduous). Larch \( \text{Larix decidua} \) was the only deciduous gymnosperm, while the N-fixing group includes two native alder species (\( \text{Alnus incana} \) and \( \text{Alnus glutinosa} \)) as well as one invasive species from North America (\( \text{Robinia pseudacacia} \)).

For each plot, we also assembled a set of environmental variables, including slope, aspect, mean annual temperature, annual precipitation, and a drought index. Slope and aspect were measured in each plot using a clinometer and compass, respectively. The climate variables were calculated using daily data from MeteoSwiss weather stations, which were first interpolated to a 100 m resolution using a digital elevation model and the Daymet software from Thornton et al. (1997). The mean annual temperature was then calculated by averaging the daily values observed between 1983 and 1995. The drought index was calculated by taking the difference between the daily precipitation and potential evapotranspiration, then averaging across the same time period. Potential evapotranspiration was calculated following T urc (1961) as

\[
\text{ETP} = \sum_{i=1}^{n} \left( \frac{10000}{A_i} \right) \text{BA}_i \text{BA}_i, \text{A}_{i}, \text{A}_{i,\text{g}}, \text{G}_{\text{max}}, \text{A}_{i}, \text{G}_{i}, \text{uBA}_{i}
\]

Data processing

For each species, we calculated the basal area (\( \text{BA}_i \)) and growth in basal area (\( \text{G}_i \)) at the plot level:

\[
\text{BA}_i = \sum_{i=1}^{n} \frac{10000}{A_i} \text{BA}_i \tag{1}
\]

\[
\text{G}_i = \sum_{i=1}^{n} \frac{10000}{\text{BA}_i} \text{A}_{i,\text{g}} \tag{2}
\]

where \( n_i \) is the number of individuals of species \( s, \) \( \text{BA}_i \) is the basal area (m²) of tree \( i \) in the first inventory, \( A_i \) is the area (m²) of the sample plot for tree \( i \) (trees greater than 36 cm DBH were sampled in larger plots), 10 000 is the number of square meters in a hectare, \( \text{BA}_i \) is the annual basal area increment (calculated using the amount of time that elapsed between the first and second inventory), and \( \text{G}_i \) is the basal area increment (m² ha⁻¹ year⁻¹) of a species cohort.

Together, these two variables were used to estimate the relative growth rate of each species, or the growth rate per unit basal area, as explained below. Note that this growth metric does not account for differences in wood density among species or functional groups. Wood density of angiosperms is generally higher than that of gymnosperms, so angiosperms accrue more mass per unit growth in basal area. This difference between angiosperms and gymnosperms should be kept in mind when interpreting the rate of basal area growth.

Trait-based model of asymmetric interactions

Similar to Kunstler et al. (2016), we estimate a set of 'pairwise dissimilarity effects' that quantify how binary trait differences alter the intensity of competition between pairs of functional groups. For example, our dissimilarity effects would allow deciduous species to reduce the suppression of evergreen species, compared to the suppression that two evergreen species exert on one another in a purely evergreen stand (given that shade is cast throughout the year). However, our model differs in two specific ways. First, our dissimilarity effects allow for asymmetric interactions in which only one species benefits from the interaction. For example, our model allows for the possibility that evergreen species do not have an equivalent effect on deciduous species (the interaction is non-reciprocal). Second, we focus on binary traits because they can be used to assign species to discrete functional groups, unlike continuous traits such as specific leaf area (Kunstler et al. 2016). This approach allows us to determine whether functional group diversity enhances productivity independently of species diversity (Reich et al. 2004, Mouillot et al. 2011, Sapajnas et al. 2014). Furthermore, this allows us to draw general conclusions that can be readily interpreted by foresters and modelers who use functional groups to implement models or management strategies.

In its most basic form, the model quantifies the growth rate of a species cohort as a negative exponential function of the plot basal area (BA):

\[
\text{G} = \text{BA}_i \left[ \text{G}_{\text{max}} e^{-uBA_i} \right] \tag{3}
\]
level of individual trees, as Kunstler et al. (2016) did. Rather, we calculated the growth in basal area of all the trees in a plot that belong to a given species.

To facilitate linear regression analysis, we first log transformed Eq. 3 to linearize the relationship between growth and competition:

$$\log G = \log BA_t + \log G_{max} - uBA$$ (4)

Then, we included various fixed and random effects to allow the maximum growth rate to vary with environmental conditions:

$$\log G_{max} = \alpha + \beta T + \gamma S + \delta A + \epsilon_p + \epsilon_s$$ (5)

where $\log G_{max}$ is the maximum relative growth rate of the species cohort $s$ in plot $p$, and the Greek letters are estimated regression coefficients.

The first four terms in Eq. 5 specify how maximum growth varies around the intercept ($\alpha$) as a function of mean annual temperature ($T$), slope ($S$), and aspect ($A$). The remaining terms, $\epsilon_p$ and $\epsilon_s$, are normally-distributed random effects (with a mean of zero) that allow growth to vary among species and plots. Note that we included species as random effects because our goal was to quantify differences in growth among functional groups, rather than differences in growth among species per se.

We did not include trait-specific terms in Eq. 5 because preliminary analyses indicated that the functional groups do not differ in their maximum growth rate (an assumption that we tested along with several others, as explained further below). However, given the difference in wood density between gymnosperm and angiosperms, one can assume that broadleaf species accrue more mass per unit growth in basal area.

Differences in relative growth do, however, emerge under competition. Thus, we added two terms to Eq. 4 to allow the suppression of the focal species to vary not only with the competition. Thus, we added two terms to Eq. 4 to allow species accrue more mass per unit growth in basal area.

Accounting for the effect of temperature

According to the stress gradient hypothesis, species are more sensitive to intraspecific competition than they are to interspecific competition (both all else being equal), since the basal area of the focal species (BA) is also included in BA (see Supplementary material Appendix 2 for further explanation). The last term in Eq. 6 includes a set of 'pairwise dissimilarity effects' that quantify the positive or negative effect of neighbors possessing traits that the focal species does not possess ($t \neq f$). These pairwise dissimilarity effects ($p$) fall into one of three categories:

Exacerbation: The trait exacerbates the suppression of the focal species, compared to the suppression exerted by a heterospecific competitor with the same traits as the focal species. Note that the term 'dissimilarity effect' specifically refers to interactions between functional groups, because this extra competitive effect is not exerted on species that share the same traits (belong to the same functional group). Also note that the term 'pairwise effect' refers to interactions between specific pairs of functional groups, so a functional group may exert several such dissimilarity effects, one for each trait defining the group.

Facilitation: The trait offsets the effect of competition, thereby facilitating the growth of the focal species. For example, N-fixing neighbors actually increase the growth of non-fixing species, indicating that the supply of extra nitrogen more than offsets any competitive effects, such as shading. Again, note that this facilitative effect does not benefit species that share the same traits as the neighbor. Also note that facilitation is not necessarily reciprocal, since two separate dissimilarity effects were estimated for each interaction (e.g. $\rho_{N\text{-fixing}}$ and $\rho_{non\text{-fixing}}$), one of which can be negligible (e.g. $\rho_{non\text{-fixing}}$).

Amelioration: The trait ameliorates the suppression of the focal species, compared to the suppression exerted by a heterospecific competitor with the same traits as the focal species. For example, deciduous species may suppress evergreen species less than evergreen species suppress one another (given that they cast shade throughout the year). This will result in overyielding (complementarity) provided that evergreen species do not suppress deciduous species more than deciduous species suppress one another (exacerbation), in which case the two asymmetric effects may cancel one another. It is important to note that Kunstler et al. (2016) did not allow for asymmetry because they only estimated one parameter that applies to both of the interacting species, affecting the suppression of both in proportion to the absolute value of the difference of the continuous trait values.
where the sign of $\lambda$ denotes whether the dissimilarity effect increases or decreases with temperature, and the sign of $\rho$ determines whether the dissimilarity effect is positive or negative at low temperatures. Note that if $\lambda$ and $\rho$ differ in sign, then the dissimilarity effect may switch from positive (amelioration, facilitation) to negative (exacerbation) as temperature increases (or vice versa).

### Alternative models and comparison of AIC values

We fitted our model in R (<www.r-project.org>) using the lme4 package for mixed effects models (Bates et al. 2015), and calculated Akaike’s information criterion (AIC) to compare it to various alternative models (Supplementary material Appendix 3). We found that the model described above (Eq. 5, 7) had the lowest AIC, indicating that it is the most parsimonious model, and that additional terms did not significantly improve model fit (Supplementary material Appendix 4). Finally, we also used AIC comparisons to assess terms for individual traits (e.g. $P_{\text{non-fixing}}$) and dropped them from the model if including them did not significantly improve the fit of our model based on AIC comparisons.

### Calculating the growth rate of mixtures relative to monocultures

We used the trait-based model (Eq. 5, 7) and the estimated parameters to quantify the magnitude of overyielding in two-species mixtures. We first calculated the growth rate of mixtures and monocultures of the two species, assuming that species from the same functional group have the same growth rate: while any given species pair may differ in growth, the average difference between species belonging to the same functional group is zero, because the mean of the random species effects is zero. Then, we calculated the percentage increase in growth of mixed stands relative to a monoculture, assuming a standardized total basal area of 30 m$^2$ ha$^{-1}$ for both mixtures and monocultures as basis for comparison. Finally, we plotted the increased growth of mixtures (y-axis) as a function of stand composition, as quantified by the portion of basal area comprised by one of the two species (x-axis).

### Data deposition

Long-term storage and availability of the data (<https://doi.org/10.21258/1000001>) is guaranteed by Swiss law (SR 510.620 and in the ‘Bundesgesetz über die Archivierung’ SR 152.1). Tables with the results of the four Swiss NFIs are freely available for download from the website <www.lfi.ch/resultate/>, while the complete list of available tree- and plot-level attributes can be found at <www.lfi.ch/dienstleist/katalog.php?lang=de>. Plot and tree data from the Swiss NFI can be provided free of charge within the scope of a contractual agreement (<www.lfi.ch/dienstleist/daten-en.php>).

### Results

For all species, growth declined at the same rate with increasing abundance of heterospecific neighbors, provided they were in the same functional group (Table 1), reaching 49% of the maximum rate at a basal area of 40 m$^2$ ha$^{-1}$ (Fig. 1). The additional effect of intraspecific competition varied among functional groups, since broadleaf species were more sensitive to intraspecific competition than needleleaf

Table 1. Estimated parameters of a trait-based model of competition in mixed gymnosperm–angiosperm forests (Eq. 5, 7). Parameters $\alpha$, $\beta$, $\gamma$, and $\delta$ quantify the effect of environmental conditions on the maximum growth rate (Eq. 5). Parameter $\mu$ (Eq. 7) quantifies the competitive effect of heterospecific neighbors with the same traits as the focal species (black line in Fig. 1). Parameter $\pi$ (Eq. 7) quantifies the incremental competitive effect of conspecific neighbors (lighter lines in Fig. 1). Parameters $\rho$ and $\lambda$ (Eq. 7) determine whether neighbors with different traits decrease (or increase) suppression (Fig. 3, 5), relative to that exerted by heterospecific neighbors with the same traits (black line in Fig. 3, 5). Note that the lower and upper bounds are 95% confidence limits, and that terms for individual traits were dropped from the model (e.g. $P_{\text{non-fixing}}$) if including them did not significantly improve model fit.

<table>
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<tr>
<th>Equation</th>
<th>Symbol</th>
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species (Table 1). For example, in monocultures with a basal area of 40 m$^2$ ha$^{-1}$, the growth rate of broadleaf species was reduced to 25% of the maximum, whereas the growth of needleleaf species was only reduced to 37% of the maximum growth rate (Fig. 1).

Since broadleaf species are more sensitive to intraspecific competition, they respond more to the alleviation of intraspecific competition. At 40 m$^2$ ha$^{-1}$, for example, broadleaf species grew twice as fast when surrounded by other broadleaf species, increasing from 25% to 49% of the maximum rate (Fig. 1). Thus, 50/50 mixtures of two different broadleaf species were 27% more productive than broadleaf monocultures (Fig. 2). In contrast, needleleaf species grew only 32% faster when surrounded by other evergreen species, increasing from 37% to 49% of the maximum rate (Fig. 1). Thus, 50/50 mixtures of two needleleaf species were only 11% more productive than needleleaf monocultures (Fig. 2).

These yield curves are symmetrical along the x-axis because there are no dissimilarity effects, and because both

**Figure 1.** Growth suppression due to inter- and intraspecific competition among species that share the same traits (belong to the same functional group). The distance between the black line (interspecific competition) and the other two lines reflects the incremental strength of intraspecific competition: broadleaf species are more sensitive to intraspecific competition than needleleaf species. The vertical lines denote 95% confidence intervals (in subsequent figures as well).

**Figure 2.** Overyielding in two-species mixtures of broadleaf species and two-species mixtures of needleleaf species, calculated using the estimated parameters (Table 1) of the trait-based model of competition (Eq. 5, 7). Increased growth is the percentage increase in growth of broadleaf and needleleaf mixtures compared to their respective monocultures (assuming basal areas of 30 m$^2$ ha$^{-1}$). The increased growth of broadleaf mixtures is greater because broadleaf species are more sensitive to intraspecific competition (Fig. 1). Since two species from the same functional group do not exert dissimilarity effects on one another, overyielding is the result of alleviating intraspecific competition.
monocultures of the same functional group are assumed to have the same growth rate. We made this assumption because the mean of the random species effects is zero, and because the goal was simply to demonstrate that overyielding is caused by the alleviation of intraspecific competition. However, adding random species differences would reduce the magnitude of overyielding, and this effect declines as the difference in growth between monocultures increases (all else being equal). Large differences would render mixtures less productive than the most productive monoculture. It is also important to note that the magnitude of overyielding varies with the metric used to calculate the mixing proportions (Pretzsch 2005, Forrester and Pretzsch 2015).

**Dissimilarity effect of N-fixing species**

N-fixing species facilitated the growth of non-fixing species (Fig. 3), and this effect was independent of temperature (Table 1), indicating that the supply of extra nitrogen more than offsets any negative effects of heterospecific competition, regardless of temperature. However, the dissimilarity effects were non-reciprocal, because non-fixing species exerted no significant dissimilarity effects on N-fixing species, though they did suppress their growth as heterospecific competitors (i.e. as different deciduous species).

Mixing N-fixing angiosperms with non-fixing angiosperms results in substantial overyielding (Fig. 4). 50/50 mixtures of N-fixing and non-fixing species are 50% more productive than monocultures of either functional group, because N-fixing species facilitate the growth of non-fixing species (Fig. 3). However, about half of the overyielding is due to the alleviation of intraspecific competition, as shown by the relative height of the lower curve, which excludes the dissimilarity effect.

**Dissimilarity effects of evergreen and deciduous species**

There was no evidence of complementarity between evergreen and deciduous species. Deciduous species exerted no significant dissimilarity effects on evergreen species (Table 1), indicating that deciduous species do not reduce the suppression of evergreen species, compared to that exerted by other evergreen species. For example, mixing larch with other gymnosperms does not reduce the effect of heterospecific competition among evergreen species, even though evergreen species cast shade on one another throughout the year (further discussion in Supplementary material Appendix 5). Thus, mixing larch with other gymnosperms only results in overyielding due to the alleviation of intraspecific competition (Fig. 2).

**Dissimilarity effects of needleleaf and broadleaf species**

The interactions between needleleaf and broadleaf species depended strongly on temperature (Table 1). At cold temperatures (3°C annual mean), they both exerted a positive dissimilarity effect on one another, though it did not amount to facilitation. Rather, they ameliorated the effect of heterospecific competition, indicating that needleleaf species suppress broadleaf species less than broadleaf species suppress one another (Fig. 3), and vice versa (Fig. 5). Thus, in montane forests, mixtures were up to 15% more productive than needleleaf monocultures (Fig. 6), which are more productive than broadleaf monocultures, because needleleaf species are less sensitive to intraspecific competition (Fig. 1).

In lowland forests, needleleaf species also ameliorated the effect of competition on broadleaf species (Fig. 3), because this positive effect increased with temperature (Table 1). In contrast, the positive effect of broadleaf species decreased with temperature (Table 1), such that the sign of the interaction effect was negative in lowland forests. Thus, broadleaf species exacerbate the effect of competition on needleleaf species.

**Figure 3.** Dissimilarity effects on the growth of broadleaf species. The black line is a reference case (also shown in Fig. 1) quantifying the effect of heterospecific neighbors with the same traits. The other lines indicate whether neighbors with different traits decrease (or increase) the suppression of the broadleaf species, relative to that exerted by heterospecific neighbors with the same traits (black line).
species (Fig. 5), completely offsetting the positive effect that needleleaf species have on broadleaf species, such that needleleaf-broadleaf mixtures were not more productive in lowland forests (Fig. 6).

Discussion

It is generally recognized that complementarity arises when one species reduces the suppression of another species (and vice versa), particularly when the species belong to functional groups that possess markedly different traits. Yet, many pairwise replacement studies do not explicitly quantify the intensity of competition and how it varies with trait differences (Uriarte 2010, Kunstler et al. 2012, Kunstler et al. 2016, Levine 2016). As a result, it often remains uncertain why, and in what combinations, mixtures are more productive than monocultures. In particular, it remains uncertain whether mixing gymnosperms and angiosperms increases productivity due to the differences in phenology and leaf morphology, or unknown niche differences between species that happen to belong to different functional groups.

Figure 4. Overyielding in two-species mixtures of N-fixing and non-fixing angiosperms, both with ($\rho > 0$) and without the dissimilarity effect ($\rho$ set to 0). Increased growth is the percentage increase in growth of mixtures relative to monocultures (assuming a basal area of 30 m$^2$ ha$^{-1}$), and was calculated using the estimated parameters (Table 1) of the trait-based model of competition (Eq. 5, 7). Note that about half of the increased growth of mixtures is due to the alleviation of intraspecific competition, as shown by the relative height of the lower curve, which excludes the dissimilarity effect.

Figure 5. Dissimilarity effects on the growth of needleleaf species. The black line represents the reference case (also shown in Fig. 1) quantifying the effect of heterospecific neighbors with the same traits. The dashed lines indicate whether neighbors with different traits decrease (or increase) the suppression of needleleaf species, relative to that exerted by heterospecific neighbors with the same traits (black line).
In order to dispel this uncertainty, we estimated a set of ‘functional dissimilarity effects’ that quantify how trait differences reduce the intensity of competition between functional groups. Our method allows for interactions that are both asymmetric and non-reciprocal, and it allows us to determine the extent to which overyielding is caused by the alleviation of intraspecific competition. Our results show that both asymmetric and non-reciprocal interactions occur between the main functional groups of Swiss tree species, including needleleaf and broadleaf species (Table 1, Fig. 1, 3). However, we found no evidence of complementarity between evergreen and deciduous species.

Dissimilarity effects have long been considered a key mechanism by which traits might affect competition (MacArthur and Levins 1967), but evidence for them is limited (Mayfield and Levine 2010). While the recent global analysis by Kunstler et al. (2016) found that competition within species was stronger than between species, they also found that the degree of trait dissimilarity between species had little influence in reducing competition. In particular, they found that the intensity of competition does not vary with continuous differences in specific leaf area, contrary to the dissimilarity effects between needleleaf and broadleaf species reported here. This discrepancy likely reflects the fact that their model did not allow for asymmetry, because they only estimated one parameter that applied to both of the interacting species jointly, ameliorating the suppression of both in proportion to the absolute value of the difference in continuous trait values.

Facilitation by nitrogen fixers

It is well known that certain functional groups exert a profound and asymmetric influence on competition and productivity. N-fixers can acquire anywhere from 10% to nearly 100% of their nitrogen intake from the atmosphere, which is made available to neighboring plants through decomposition, root exudation, and mycorrhizal transfer (Rothe and Binkley 2001, Richards et al. 2010). Indeed, we found that N-fixing species facilitate the growth of other species (but not vice versa) such that mixtures are 50% more productive than monocultures. This effect was independent of temperature (Table 1), but it remains uncertain whether overyielding is so large at the coldest end of the temperature gradient, since there were only three plots with nitrogen fixers at temperatures below 4.5°C (Supplementary material Appendix 1).

These results are consistent with other studies that show mixtures with alder species are more productive than monocultures without alder, particularly on poor soils (Binkley et al. 1992, Mason and Connolly 2013). It is also consistent with a recent meta-analysis of 18 studies which found that N-fixing mixtures were significantly more productive than monocultures in most studies (Forrester et al. 2006). However, we found that half of the overyielding in N-fixing mixtures is due to the alleviation of intraspecific competition, and therefore attributable to unknown differences between species that happen to belong to different functional groups. Thus, caution is warranted in interpreting pairwise studies that fail to disentangle the effects of intraspecific competition and nitrogen fixation, lest overyielding be falsely attributed to nitrogen fixation.

Mixing evergreen and deciduous gymnosperms

We found no evidence for temporal niche complementarity among gymnosperms. In particular, we found that mixing the deciduous larch with other gymnosperms species only increases productivity due to the alleviation of intraspecific competition. Other studies have also reported overyielding...
when larch is mixed with other gymnosperms (Morgan et al. 1992, Cameron and Watson 2000, Pretzsch 2005), but these studies did not attempt to disentangle the effects of intraspecific competition and seasonal light partitioning. Thus, the evidence for temporal niche complementarity between gymnosperms remains inconclusive.

However, recent studies have shown that complementarity is more likely to occur in vertically stratified stands in which understorey trees belong to a different species or functional group than overstory trees (Dănescu et al. 2016, Madrigal-González et al. 2016). This suggests that vertical stratification of evergreen–deciduous stands (i.e. an evergreen understory below a deciduous canopy) may allow them to intercept more light throughout the year than stands comprised of only one of the functional groups. Yet, our method does not account for tree size or stand structure, so it must be modified to assess whether vertical stratification alleviates the size asymmetry of competition for light.

A long-lasting debate about mixing gymnosperms and angiosperms

The complementarity of gymnosperms and angiosperms has been actively debated since the dawn of silviculture in Europe, with early practitioners arguing both for and against mixed stands (Pretzsch 2005). The subsequent establishment of conifer stands throughout Europe attests to the fact that they provide higher volume yields in monoculture (Pretzsch et al. 2015), which is consistent with our results and other studies suggesting that conifer stands are more productive (Augusto et al. 2015). However, the relative productivity of mixed stands has remained a topic of debate until the present.

Interest in this topic has surged in recent years because conifer stands are being converted back to mixed stands at an ever-increasing rate (Knöke et al. 2008). Thus, numerous studies have examined the productivity of mixed stands comprised of common temperate species such as Norway spruce and European beech (Jones et al. 2005, Pretzsch 2005). These studies have found that some pairs exhibit overyielding across a wide range of conditions, such as Scots pine and European beech (Pretzsch et al. 2015), while others only under certain conditions, such as Norway spruce and European beech (Pretzsch and Schütze 2009, Töigo et al. 2015). Again, these pairwise studies generally do not attempt to disentangle the effects of phenology and leaf morphology, and many do not rule out the possibility that overyielding simply reflects unknown niche differences between species that happen to belong to different functional groups. Yet, some studies do identify a mechanism that causes positive interactions between the two species, but often it is not necessarily related to the fact that one is a gymnosperm and the other is an angiosperm, such as differences in shade tolerance (Pretzsch 2005). Thus, it remains uncertain why mixing gymnosperms and angiosperms increases productivity under certain circumstances.

Stress gradient hypothesis

We found that dissimilarity effects only increase the productivity of needleleaf–broadleaf mixtures at one end of the altitudinal temperature gradient. This result is consistent with the stress gradient hypothesis (Maestre et al. 2009, Jucker et al. 2016), as well as with studies showing that the strength of the correlation between diversity and productivity increases as temperature decreases with latitude (Paquette and Messier 2011, Potter and Woodall 2014, Wu et al. 2015, Jucker et al. 2016). This suggests that altitudinal and latitudinal trends may reflect the same underlying mechanisms, and perhaps temporal light partitioning is not one of them. Yet, the mechanisms underlying the complementarity of angiosperms and gymnosperms remain uncertain, and none of the other hypotheses invoke productivity or temperature as an important factor.

Other than temporal light partitioning (Sapijanskas et al. 2014), the most common hypothesis is that overyielding is the result of vertical stratification of complementary crown shapes, which allows mixed stands to fill canopy space more effectively than stands comprised of a single crown shape, particularly if crowns exhibit greater plasticity in mixed stands (Pretzsch 2014, Jucker et al. 2015, Pretzsch and Schütze 2016). This hypothesis generally assumes that both gymnosperms and angiosperms benefit from stratification and crown plasticity, regardless of the productivity of the environment. Indeed, the positive effect of mixing on canopy packing is strongly conserved across the full latitudinal gradient of Europe (Jucker et al. 2015). Other light partitioning hypotheses emphasize differences in physiology and the display of foliage (Ishii and Asano 2010), while water and soil nutrients have also been hypothesized to allow for spatial resource partitioning (Pretzsch et al. 2015). However, most hypotheses are invoked to explain overyielding and therefore assume the interactions to either be symmetric and positive or non-reciprocal, rather than asymmetric under certain conditions, as we found in lowland temperate forests.

Asymmetry and the role of litter quality

Pairwise studies have also reported negative interactions, including asymmetric interactions, in which one species suppresses another, but is itself unaffected, or even benefits from the interaction (Jones et al. 2005, Pretzsch 2005). While some studies report that broadleaf species benefit at the expense of needleleaf species (Mård 1996, Valkonen and Valsta 2001, Pretzsch 2005), as we found in lowland forests, the evidence is by no means consistent across studies. However, the lack of consistent evidence for asymmetric interactions is not surprising, given that pairwise interactions are generally expected to alleviate intraspecific competition, potentially offsetting any negative effects (Fig. 5b), which would not be evident without using methods such as those presented here. Thus, it also remains uncertain why angiosperms benefit at the expense of gymnosperms under certain conditions.
Leaf litter quality has a profound influence on decomposition and nutrient cycling (Hättenschwiler 2005, Cornwell et al. 2008), and the quality of needle and broadleaf litter could not be more different. Needleleaf litter generally has higher lignin concentration, and lower concentrations of N and P, which are released more slowly because the rate of decomposition is roughly half that of broadleaf litter (Cornwell et al. 2008, Augusto et al. 2015). Thus, at first glance it seems reasonable that litter quality could mediate the interactions between gymnosperms and angiosperms through its effect on soil resources. For example, if litter mixing effects were strictly additive (Ball et al. 2008), then the addition of broadleaf litter would increase the rate of nutrient cycling in needleleaf stands, which is consistent with our observation that broadleaf species ameliorate the suppression of needleleaf species in montane forests. However, the addition of needleleaf litter would slow the rate of nutrient cycling in broadleaf stands, which is inconsistent with our observation that needleleaf species ameliorate the suppression of broadleaf species.

Yet, it is possible that non-additive litter mixing effects could promote complementary interactions between gymnosperms and angiosperms (Gessner et al. 2010). For example, microbes and detritivores can make complementary use of resources by obtaining different resources from low- and high-quality litter, particularly when nutrients are transported between the two substrates via fungal hyphae (Schimel and Hättenschwiler 2007). This complementary use of resources can accelerate decomposition and nutrient turnover in mixed litter (Hättenschwiler 2005), which may in turn promote complementarity between gymnosperms and angiosperms, provided they both benefit from the non-additive litter mixing effect. Our results suggest that they both benefit from the non-additive litter mixing effect in montane, boreal-type forests, whereas angiosperms benefit at the expense of gymnosperms in lowland temperate forests. While positive non-additive effects on decomposition are widely observed in litter-mixing experiments, negative and neutral interactions have been reported as well, and there is no consensus regarding mixtures of needle and broadleaf litters (Hättenschwiler 2005, Gessner et al 2010). Thus, it remains uncertain whether litter quality mediates the interactions between gymnosperms and angiosperms through its effect on soil resources. Furthermore, it remains unclear why mixing litters and accelerating nutrient turnover would only favor angiosperms in lowland forests.

However, it is widely recognized that broadleaf angiosperms are able to acquire and recycle resources faster than needleleaf gymnosperms, whose conservative use of resources allows them to dominate in less productive environments (Grime 2006, Coomes et al. 2005). Thus, it is possible that accelerating nutrient turnover only favors angiosperms in lowland forests because this advantage is only realized in more productive environments. Indeed, the fact that angiosperms profit from increased nutrient turnover has been recently advanced to explain the historical displacement of gymnosperms from productive environments, otherwise known as Darwin’s abominable mystery (Bond 1989, Berendse and Scheffer 2009).

The need for experiments

We sought to generalize the results of pairwise replacement studies by examining the competitive interactions observed in an inventory dataset that encompasses a broad variety of species, functional groups, and climatic conditions. While our regression-based method revealed that complementarity arises from dissimilarity effects that are both asymmetric and non-reciprocal, it does not allow us to elucidate the underlying mechanisms. Furthermore, it would be difficult to separate the effect of variables that co-vary along the altitudinal gradient, such as temperature and soil resource availability. Thus, there is a need to conduct controlled biodiversity–productivity experiments to study overyielding in gymnosperm–angiosperm mixtures, similar to those conducted in seasonal tropical forests that exhibit temporal niche complementarity between evergreen and deciduous angiosperms (Sapijanskas et al. 2014). While these experiments suffer their own limitations, due to the long life span of trees and slow dynamics of forests, using high-density mixtures holds promise for elucidating the mechanisms underlying the dissimilarity effects identified in this study (Tobner et al. 2014).

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Supplementary material (available online as Appendix oik-05360 at <www.oikosjournal.org/appendix/oik-05360>). Appendix 1–5.