Partitioning changes in ecosystem productivity by effects of species interactions in biodiversity experiments

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Abstract

Species interactions affect ecosystem productivity. Positive interactions (resource partitioning and facilitation) increase productivity while negative interactions (species interference) decrease productivity relative to the null expectations defined by monoculture yields. Effects of competitive interactions (resource competition) can be either positive or negative. Distinguishing effects of species interactions is therefore difficult, if not impossible, with current biodiversity experiments involving mixtures and full density monocultures.

To partition changes in ecosystem productivity by effects of species interactions, we modify null expectations with competitive growth responses, i.e., proportional changes in individual size (biomass or volume) expected in mixture based on species differences in growth and competitive ability. We use partial density (species density in mixture) monocultures and the competitive exclusion principle to determine maximum competitive growth responses and full density monoculture yields to measure species ability to achieve maximum competitive growth responses in mixture. Deviations of observed yields from competitive expectations represent the effects of positive/negative species interactions, while the differences between competitive and null expectations reflect the effects of competitive interactions.

We demonstrate the effectiveness of our competitive partitioning model in distinguishing effects of species interactions using both simulated and experimental species mixtures. Our competitive partitioning model enables meaningful assessments of species interactions at both species and community levels and helps disentangle underlying mechanisms of species interactions responsible for changes in ecosystem productivity and identify species mixtures that maximize positive effects.

Keywords: competitive interaction, null expectation, competitive expectation, biodiversity effect, competitive partitioning

Species interactions and ecosystem productivity

Detecting changes in ecosystem productivity with biodiversity and understanding how these changes are affected by mechanisms of species interactions has been a central focus in ecology for decades (Loreau, 2000; Loreau and Hector, 2019; Mahaut et al., 2020). However, effective methods are lacking (Drake, 2003; Forrester and Pretzsch, 2015; Jaillard et al., 2018; Barry et al., 2019; Loreau and Hector, 2019; Bourrat et al., 2023). The method of additive partitioning was developed from the covariance equation to quantify changes in ecosystem productivity by comparing species performance in mixture with those expected from their monocultures using a replacement design (de Wit, 1960; Loreau and Hector, 2001; Barry et al., 2019). The resultant changes in ecosystem productivity (commonly referred to as net biodiversity effects) are mathematically decomposed into additive components, namely the complementarity effect (CE) measuring community average response and the selection effect (SE) measuring interspecies differences (Loreau and Hector, 2001; Forrester and Pretzsch, 2015; Loreau and Hector, 2019). CE ad SE are widely used to examine mechanisms of species interactions responsible for biodiversity effects, i.e., CE for positive interactions and SE for competitive interactions (Loreau and Hector, 2001; Petchey, 2003; Polley et al., 2003; Montès et al., 2008; Barry et al., 2019; Hagan et al., 2021; Feng et al., 2022), despite that neither of the additive components can be linked to specific effects of species interactions (Petchey, 2003; Hooper et al., 2005; Montès et al., 2008; Loreau et al., 2012; Forrester and Pretzsch, 2015; Loreau and Hector, 2019; Hagan et al., 2021; Bourrat et al., 2023).

Among the interspecific interactions in plants, positive interactions (resource partitioning and facilitation or collectively referred to as complementarity) increase productivity and negative interactions (species interference or interference competition) decrease productivity relative to

the null expectations, i.e., species yields expected in mixture based on composition (relative yield) and full density monoculture yields (Loreau, 2000; Loreau and et al., 2005; Barry et al., 2019). Uncertainty comes with effects of competitive interactions (i.e., resource competition) that are positive for more competitive species and negative for less competitive species (Aschehoug et al., 2016; Barry et al., 2019). For example, when a highly competitive and less competitive species are mixed, more resources flow to the more competitive species. The yield gain of more competitive species from increases in resource availability (resources per capita) often exceeds the yield loss of less competitive species from decreases in resource availability (Huston, 1997; Tilman et al., 1997; Wardle, 1999; Montazeaud et al., 2018; Pillai and Gouhier, 2019), resulting in positive deviation from the total expected yield of both species (i.e., positive biodiversity effect). Competitive interactions can also result in negative biodiversity effects if the less competitive species suffers more than the more competitive species benefits.

The positive effects of competitive dominance on ecosystem productivity can be illustrated with species mixture data. In the situations of both simulated and experimental mixtures with two species, the partial density monoculture yield of the more competitive species exceeded the total expected yield of both species in 32 of the 35 mixtures (***Table 1***), meaning that a higher productivity expected for a given species mixture under the null hypothesis can be generally achieved by removing less competitive species from the mixture (***Table S1; Table S2***). In other words, the positive biodiversity effects of mixtures detected through the null expectation can be obtained from the monocultures of more competitive species at partial (lower) densities. These positive biodiversity effects, however, result from competition-induced changes in resource availability, i.e., the yield gain of more competitive species from all resources in the mixture exceeds the total yield loss expected for the less competitive species, and are not related

to effects of positive species interactions. Competitive interactions are the predominant type of interspecific relationships in plants and occur in all mixtures where constituent species are competitively different (Goldberg and Barton, 1992; Pillai and Gouhier, 2019). Reporting positive biodiversity effects, without indication of possible contributions from competitive interactions, can lead to unrealistic expectations for effects of positive interactions.

Given the limits of the additive partitioning in deciphering mechanisms of changes in ecosystem productivity (Loreau and Hector, 2001; Petchey, 2003; Forrester and Pretzsch, 2015), some alternative methods have been explored to identify underlying mechanisms. This includes the use of metrics such as relative yield totals (Hector, 1998; Roscher and Schumacher, 2016) and transgressive overyielding or superyielding (Drake, 2003; Forrester and Pretzsch, 2015; Špaèková and Lepš, 2001), the multiplicative partitioning or statistical analyses to separate effects of species interactions and species composition (Kirwan et al., 2009; Jaillard et al., 2018, 2021; Chen et al., 2020), the identification of relative species influences via measurement of competitive interactions (Montès et al., 2008; Mahaut et al., 2020; Brun et al., 2022), or influences of species diversity, composition, and density on net biodiversity effects (Polley et al., 2003; Roscher and Schumacher, 2016; Jaillard et al., 2018; Mahaut et al., 2020; Tatsumi and Loreau, 2023). However, although these methods may indicate the presence of strong positive or competitive interactions or connections of the additive components with niche and fitness differences (Carroll et al., 2011; Turnbull et al., 2013; Godoy et al., 2020), they are not capable of quantifying changes in ecosystem productivity by species interactions at species or community level.

Here, we present the competitive partitioning model, a new framework for assessing effects of species interactions on ecosystem productivity based on null expectations and

competitive growth responses, the proportional changes of individual size (biomass or volume) from full density monocultures to mixtures expected from species differences in growth and competitive ability (***Figure 1***). Current biodiversity experiments are generally established based on a replacement design with equal density across mixtures and monocultures (Sackville Hamilton, 1994) and do not provide data for estimating competitive growth responses. Thus, we applied this new methodological approach to simulated data generated with the GYPSY model (Huang et al., 2009) for trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) tree mixtures and greenhouse experimental data from grassland mixtures (Mahaut et al., 2020) (***Table 1***). We used partial density (species density in mixture) monocultures and the competitive exclusion principle to determine maximum competitive growth responses and full density monoculture yields to measure species ability to compete for resources and achieve maximum competitive growth responses in mixture. Our objectives are to (1) demonstrate the power of this new framework in distinguishing effects of species interactions responsible for changes in ecosystem productivity, (2) illustrate how the mechanisms of changes in ecosystem productivity differ between the assessments with competitive and additive partitioning models, and (3) assess the effects of competitive interactions on ecosystem productivity relative to those of other species interactions.

Competitive expectation

Under the null hypothesis, species in mixture are assumed to be competitively equivalent (i.e., absence of interspecific interactions) and species growth (or any other function) stays the same in mixture as in monocultures (Loreau and Hector, 2001). Deviations of observed yields (biomass

or volume) from total null expectation therefore produce net biodiversity effects or changes in ecosystem productivity (Loreau and Hector, 2001; Barry *et al*., 2019).

$$\sum Y_{Oi} - \sum Y_{NEi} = \sum RY_{Oi} M_{if} - \sum RY_{Ei} M_{if}$$

$$= \sum \Delta RY_i M_{if} \qquad (1)$$

Thus, the net biodiversity effect is the difference between total observed yields $\sum Y_{Oi}$ and total null expectation $\sum Y_{NEi}$, calculated from species composition (or relative yield) in mixture RY_{Ei} and full density monoculture yield M_{if}. Mathematically, the net biodiversity effect is an arithmetic mean of full density monoculture yields weighted by changes in species relative yield ΔRY_I, and results from all species interactions including positive (positive biodiversity effects), competitive (positive or negative biodiversity effects), and negative (negative biodiversity effects) interactions. Net biodiversity effects can be mathematically decomposed into an arithmetic mean (a product of mean monoculture yield by mean relative yield change) representing community average response (CE) and a covariance (between monoculture yield and relative yield change) representing interspecies differences (SE) (Loreau and Hector, 2001).

To separate effects of competitive interactions from those of other species interactions, we would need the hypothesis that constituent species share an identical niche but differ in growth and competitive ability (i.e., absence of positive/negative interactions). Competitive growth responses, i.e., proportional changes in individual size (biomass or volume) expected from full density monocultures to mixtures under this competitive hypothesis, can be determined from species differences in growth and competitive ability (***Figure 1***). The magnitudes of competitive growth responses depend on: (1) species resource needs in full density monocultures; and (2) changes in resource availability (resources per capita) from full density monocultures to

full density mixtures that are related to species composition and relative ability to compete for resources in mixture.

To estimate competitive growth response, we first determine the maximum competitive growth response $\mathrm{MG_i}$ that species can reach in a scenario of competitive exclusion (Murray, 1986) where a more competitive species completely dominates and grows like a partial density monoculture, while a less competitive species is competitively eliminated.

$$\mathrm{MG_i} = \frac{w_{ip}}{w_{if}} - 1, \text{ for more competitive species}$$

$$= -1, \text{ for less competitive species} \qquad (2)$$

Here, $\mathrm{w_{ip}}$ stands for individual size (biomass or volume) in partial density (species density in mixture) monoculture and $\mathrm{w_{if}}$ is for individual size in full density monoculture; both parameters are calculated from species monoculture yields and initial densities in partial/full density monocultures. A more competitive species gains $\frac{1}{RY_{Ei}} - 1$ in resource availability and $\frac{w_{ip}}{w_{if}} - 1$ in individual size, while a less competitive species loses 100% resource availability and size in mixture relative to full density monoculture (***Figure 1***). This simplified competitive dominance applies to mixtures where constituent species differ considerably in competitive ability, especially when competition for light is intense (Grime, 1973; Lieffers et al., 1993). In most cases, however, competitive exclusion would not occur in biodiversity experiments that are controlled in density, composition, duration, and scale. More competitive species are negatively affected by interspecific competition relative to their partial density monocultures (Holland and DeAngelis, 2009), while less competitive species are competitively suppressed relative to their null expectations, but not eliminated (Aarssen, 1989; Connolly et al., 2001; Montazeaud et al., 2018; Mahaut et al., 2020).

Next, we use relative competitive ability $\mathrm{RC_i}$ to represent species ability to compete for resources and achieve their maximum competitive growth response in mixture (Aarssen, 1989). $\mathrm{RC_i}$ is defined by the deviation of species competitive ability H_i from community average $\overline{H}_{i\notin}$ (excluding species i) relative to community maximum H_m. Competitive ability is species ability to exploit resources and can be assessed by growth attributes such as full density monoculture yields in biomass or volume (Gaudet and Keddy, 1988; Aarssen, 1989; Grace, 1990; Aschehoug et al., 2016; Montazeaud et al., 2018).

$$\mathrm{RC_i} = \frac{|H_i - \overline{H}_{i\notin}|}{H_m} \quad (3)$$

Greater competitive advantages would lead to increasingly positive competitive growth responses and larger competitive disadvantages would lead to increasingly negative competitive growth responses in mixture relative to full density monocultures.

$$\mathrm{Y_{CEi}} = \mathrm{Y_{NEi}}[1 + \mathrm{MG_i RC_i}] \quad (4)$$

Species competitive expectation $\mathrm{Y_{CEi}}$ is the yield based on null expectation $\mathrm{Y_{NEi}}$ and competitive growth response $\mathrm{MG_i RC_i}$ derived from species differences in growth and competitive ability (***Figure 1***). The term $\mathrm{MG_i RC_i}$ would be positive for more competitive species $\mathrm{MG_i} > 0$, negative for less competitive species $\mathrm{MG_i} < 0$, and zero when species are at community average or competitively equivalent $\mathrm{RC_i} = 0$. At individual species level, the deviation of observed yield $\mathrm{Y_{Oi}}$ from the competitive expectation $\mathrm{Y_{CEi}}$ can be positive (representing relaxation of interspecific competition from competitive expectation and therefore dominance of positive interactions), neutral (representing similar intra- and interspecific interactions or offset of positive and negative interactions), or negative (representing dominance of negative interactions). The differences between competitive and null expectations are competitive yield changes resulting from competitive interactions. Isolating facilitative effect from those of other positive interactions (i.e.,

resource partitioning) is also possible for individual species by comparing species' observed yield in mixture to their partial density monoculture yield, adapting the principle of additive design for biodiversity–ecosystem productivity experiments (Sackville Hamilton, 1994). At the community level, the difference in total yield between competitive expectations $\sum Y_{CEi}$ and null expectations $\sum Y_{NEi}$ of all species can be attributed to the competitive effect, whereas the difference between observed yields $\sum Y_{Oi}$ and competitive expectations $\sum Y_{CEi}$ can be attributed to the dominance of positive effects when the difference >0 or to the dominance of negative effects when the difference <0 (***Figure 1***).

Case studies

Simulated aspen and spruce mixtures

Mixed forests composed of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are widely distributed in North America (Man and Lieffers, 1999). The two species, occurring in pure and mixed stands of varying compositions in natural conditions, generally have different canopy structure, rooting depth, leaf phenology, and requirements for light, moisture, and nutrients so are considered different in niche (Man and Lieffers, 1999).

We used a growth and yield simulation system GYPSY, developed for mixed species forests in western Canada (Huang et al., 2009), to generate data required for determining competitive expectation, i.e., mixtures and monocultures at partial and full densities. We were interested in knowing how effects of species interactions may vary with stand age and composition. We chose four ages: 20, 40, 60, and 80 years, to represent young, middle-aged, pre-mature, and mature stands, and five relative yields from nearly pure aspen (90% aspen), aspen-

dominated (70% aspen), equal mixed (50% aspen), spruce-dominated (30% aspen), to nearly pure spruce (10% aspen) mixtures at average densities on fully stocked medium productivity sites (Peterson and Peterson, 1992) (***Table 1***). As GYPSY is developed from extensive field observations (Huang et al., 2009), the simulated data represent average yields in natural monocultures and mixtures of various composition and ages that may result from direct or indirect interactions between the two species (Man and Lieffers, 1999; Barry et al., 2019). Species competitive ability was approximated with stand volume in full density monocultures at site index 17 m and 14 m (height), respectively, for dominant and codominant aspen and spruce at 50 years of total age on medium productivity sites (Alberta Forest Service, 1985; Huang et al., 1994).

The partitioning of net biodiversity effects with competitive partitioning model indicated that the relative contribution of competitive interactions to net biodiversity effects decreased with age (***Figure 2a***), whereas community positive effects occurred generally in pre-mature and mature stands and more so in equal aspen and spruce mixtures (***Figure 2b***). Evidence for a facilitative effect (i.e., species observed yield in mixture > partial density monoculture yield) was only found on spruce in nearly pure mature spruce mixture (***Table 1***). Community negative effects occurred in young and middled-age mixtures where aspen did poorer than expected under the competitive expectation (***Table S1***). Averaged across all ages and compositions, the net biodiversity effect was 14.3 m^3 ha^{-1} or 14% of the average full density monoculture yield. On a relative basis, 57% of the value (8.2 m^3 ha^{-1}) was attributable to positive effects, 65% (9.3 m^3 ha^{-1}) to competitive effects and -23% (-3.2 m^3 ha^{-1}) to negative effects, compared to 63% and 37% for CE and SE with additive partitioning (***Figure 2c; Figure 2d***).

Experimental grassland mixtures

Mahaut et al. (2020) conducted an experimental study in pots with six grassland species in full and half-density monocultures, as well as in every combination of two, three and six species in mixture. The studied species vary in productivity and functional traits. We used aboveground biomass data from full and half-density monocultures, as well as all combinations of two species in full density mixtures (***Table 1***). Species competitive ability was approximated with species biomass in full density monocultures.

Competitive partitioning suggested a weak facilitative effect in two mixtures that were associated with *Lotus corniculatus*, one of the two legume species studied (***Table 1; Table S2***). Community negative effects occurred in two mixtures with *Sanguisorba minor* and between the two legumes, due to negative effects of *Sanguisorba minor* on other species and *Lotus corniculatus* on *Trifolium repens* (***Table S2***). Across all 15 two-species mixtures, the average of net biodiversity effects on aboveground biomass was 3.9 g/pot or 49% of the full density monoculture yield averaged across all species. On a relative basis, 60% (2.3 g) of the value was attributable to positive effects, 45% (1.7 g) to competitive effects, and -5% (-0.2 g) to negative effects, compared to 84% and 16% for CE and SE with additive partitioning (***Table 2***).

Comparison of additive and competitive partitioning

The competitive partitioning model provides a conceptual framework that helps establish the linkage between changes in ecosystem productivity and effects of species interactions. Under this framework, in both simulated tree and experimental grassland mixtures, net biodiversity effects were generally positive, resulting from both positive and competitive interactions. The positive competitive effects result from greater competitive yield responses of more competitive

species (Huston, 1997; Tilman et al., 1997; Wardle, 1999; Montazeaud et al., 2018), i.e., the yield gain of more competitive species from increases in resource availability exceeds the yield loss of less competitive species from decrease in resource availability, due to different competitive growth responses and full density monoculture yields (***Table S1; Table S2***). The greater competitive yield response of more competitive trembling aspen in young and middle-aged mixtures resulted in net biodiversity effects that were predominantly from competitive interactions (***Figure 2a; Figure 2b; Table S1***). A facilitative effect was rarely detected, only on spruce in nearly pure spruce mature mixture, possibly due to improved nutrient availability by aspen (Peterson and Peterson, 1992; Man and Lieffers, 1999) and in mixtures with legume *Lotus corniculatus* in grassland mixtures, likely due to improved nitrogen availability (Mahaut et al., 2020). The strong negative effect of mixing on aspen (i.e., observed yields < competitive expectations, see ***Table S1***) in young and middled-age mixtures suggests that trembling aspen originating naturally in high density does not benefit from mixing with white spruce. This is in contrast with white spruce where the deviations of observed yields from competitive expectations were generally positive, likely due to its shade tolerance and positive effects of aspen on nutrient availability (Peterson and Peterson, 1992; Man and Lieffers, 1999).

The net biodiversity effects reveal overall community yield changes from what would be expected from full density monoculture yields (Loreau and Hector, 2001; Loreau and Hector, 2019). However, the underlying mechanisms of species interactions for detected changes are uncertain, due to effects of competitive interactions that can be positive or negative. In both simulated mixed forests and experimental grassland mixtures, the partial density monoculture yield of the more competitive species exceeded the total expected yield of both species in nearly all mixtures (see ***Table S1*** and ***Table S2***), resulting in positive biodiversity effects when positive

species interactions are not involved. Such positive biodiversity effects may help understand changes in ecosystem productivity detected through the null expectation (Carroll et al., 2011; Godoy et al., 2020) but do not support the general expectation that positive changes in ecosystem productivity are associated with positive species interactions (Loreau, 2000; Drake, 2003; Hooper et al., 2005; Barry et al., 2019) or crop mixing in agriculture and forestry where interests are positive effects (Man & Lieffers, 1999; Forrester & Pretzsch, 2015; Montazeaud et al., 2018). Thus, partitioning net biodiversity effects by effects of species interactions (i.e., positive, competitive, negative effects) allows for estimating relative importance of mechanisms of species interactions responsible for changes in ecosystem productivity. This enables ecologists to determine which communities are truly benefitting from diversity in the form of positive interactions and which result from interspecies differences in growth and competitive ability. In the aspen and spruce mixtures examined, community positive effects occurred largely in pre-mature and mature mixtures (>=60 years), even though net biodiversity effects and CE were positive at nearly all stages of stand development (***Figure 2***). In grassland mixtures, two mixtures (i.e., *Dactylis glomerata* - *Sanguisorba minor* and *Lotus corniculatus* - *Trifolium repens*) had positive net biodiversity effects that resulted entirely from competitive interactions (***Table 2; Table S2***). These positive net biodiversity effects may indicate evidence for positive changes in ecosystem productivity when these changes were actually driven by differential outcomes of interspecific competition.

We demonstrate with simulated and experimental species mixtures that competitive interaction is a major source of the net biodiversity effects and affects the additive components of both CE and SE. In the scenario of partial density monocultures emulating a simplified scenario of competitive exclusion where positive net biodiversity effects resulted entirely from

competitive interactions, CE was generally negative in tree mixtures where relative yield changes were smaller with more competitive species (negative mean relative yield change) but positive in grassland mixtures where relative yield changes were greater with more competitive species (positive mean relative yield change) (***Table S1; Table S2***). In aspen-spruce mixtures, SE was either larger (age 80) or smaller (age 20, 40, and 60) than competitive effect. In the grassland communities, SE was similar to competitive effect in 3 of the 15 mixtures (*Bromus erectus* - *Lotus corniculatus*, *Dactylis glomerata* - *Lotus corniculatus*, and *Lotus corniculatus* - *Sanguisorba minor*) but substantially smaller in the remaining mixtures (***Table 2***). Even in the extreme cases where SE was nearly zero (*Bromus erectus* - *Sanguisorba minor* and *Bromus erectus* - *Trifolium repens*), competitive effect was still relatively strong, suggesting that a common assumption to attribute positive net biodiversity effects to positive species interactions when SE is close to zero (Loreau and Hector, 2001; Feng et al., 2022) is not justified. Competitive interactions amplify interspecies differences and therefore SE, while species interference on more competitive species (*Bromus erectus* - *Sanguisorba minor*) and greater positive species interactions on less competitive species (*Bromus erectus* - *Trifolium repens*) (***Table S2***) reduce SE. Our findings, along with some recent suggestions (Carroll et al., 2011; Turnbull et al., 2013; Godoy et al., 2020; Bourrat et al., 2023), do not support some common exercises that attribute positive/negative CEs to positive/negative interactions (Loreau and Hector, 2001; Petchey, 2003; Fargione et al., 2007; Barry et al., 2019; Hagan et al., 2021; Feng et al., 2022) and positive SEs to competitive interactions (Loreau, 2000; Loreau and Hector, 2001; Montazeaud et al., 2018).

Several assumptions are adopted with the development of competitive partitioning model. First, we assumed that more productive species are more competitive, which was mostly true

with the species mixtures examined in terms of species yields in mixture relative to their full density monoculture yields (***Table 1***). There were exceptions with Dactylis:Plantago and Plantago:Trifolium in grassland mixtures where less productive species Plantago based on full density monoculture yields performed better in mixtures, which may suggest positive effects on Plantago and negative effects on the other species. However, species yields in partial versus full density monocultures indicate that these exceptions resulted from the stagnation of more productive Plantago in full (high) density monocultures, due to restricted rooting volumes and supplies of water and nutrients in pots (Chung et al., 2021). The release of growth stagnation in partial density monocultures and mixtures affects not only the mechanisms of changes in ecosystem productivity assessed with competitive and additive partitioning models but also the magnitudes of the changes in ecosystem productivity detected through the null expectation (Loreau and Hector, 2001). In this case, the use of partial density monoculture yields in assessment of species competitive ability are probably more appropriate, which would increase the values of competitive effects and reduce those of positive effects based on the competitive expectations. Partial density monocultures help detect competition-related yield changes, which would be otherwise unknown. Second, we used partial density monocultures to determine maximum competitive growth responses in a simplified competitive exclusion where more competitive species are not affected and grow like partial density monocultures, while less competitive species are competitively eliminated. We assumed a linear relationship between competitive growth responses and species relative competitive ability (***Figure 1***), which should be a good approximation (Gaudet and Keddy, 1988), but may not be the most appropriate, e.g., light availability and plant height (Brüllhardt et al., 2020). Linear models can overestimate or underestimate competitive expectations of all species and affect individual species assessments

but would have limited impacts on community level assessments, due to different directions of competitive growth responses among species.

The competitive partitioning model incorporates effects of competitive interactions into the conventional null expectation and assists: (1) understanding the mechanisms of species interactions driving positive biodiversity-productivity relationships (Cardinale et al., 2012; Isbell et al., 2017) by relative contributions of positive interactions from more species of diverse niche (Tilman et al., 1997; Hooper et al., 2005) and competitive interactions from greater yield responses of more competitive and more productive species to changes in resource availability in mixture (Aarssen, 1997; Huston, 1997; Tilman et al., 1997; Pillai and Gouhier, 2019), (2) examining the mechanisms of key species in influencing ecosystem productivity by roles of competitive interactions due to their higher productivity and competitive advantages (Loreau and Hector, 2001; Mahaut et al., 2020), (3) meaningful comparisons of changes in ecosystem productivity (i.e., relative yield totals) across different ecosystems based on competitive expectations, and (4) redefining changes in ecosystem productivity such that positive changes result from positive interactions and negative changes from negative interactions (Loreau, 2000; Drake, 2003; Hooper et al., 2005). Under this competitive partitioning framework, null expectations are either raised for more competitive species with increased resource availability or lowered for less competitive species with decreased resource availability in mixture relative to full density monocultures. The magnitudes of competitive growth responses are derived from species relative competitive ability in mixture and their maximum competitive growth responses determined from full and partial density monocultures under a simplified scenario of competitive exclusion. Current biodiversity experiments do not have partial density monocultures and therefore do not provide estimates of competitive growth responses that would occur in mixture

due to interspecies differences in growth and competitive ability. However, density-size/yield relationship is one of the most extensively studied areas in ecology (Watkinson, 1980; Weiner and Freckleton, 2010). Previous research can help determine maximum competitive growth responses through density-size/yield relationships (Huang et al., 2009). This means that the competitive partitioning model can be used to investigate changes in ecosystem productivity by effects of species interactions in current biodiversity experiments established with replacement design (Loreau and Hector, 2001; Fargione et al., 2007).

Conclusions

Competitive interactions are the major source of biodiversity effects and affect the additive components of both CE and SE. The interpretations of CEs and SEs with specific effects of species interactions lack mathematical or ecological justifications. For example, attributing positive biodiversity effects solely to effects of positive interactions, as commonly seen in the literature (Loreau and Hector, 2001; Hooper et al., 2005; Fargione et al., 2007; Barry et al., 2019; Feng et al., 2022), assumes that competitive interactions are productivity-neutral (SE close to zero) (Loreau and Hector, 2001; Feng et al., 2022). This assumption is true if ecosystem productivity is defined by total resources pool (Tilman et al., 2014) but generally not true if mixture productivity is defined by species monoculture yields as with the additive partitioning (Loreau and Hector, 2001), due to the predominance of competitive interactions in interspecific relationships (Goldberg and Barton, 1992) and positive effects of competitive interactions on ecosystem productivity based on the null expectation.

The competitive partitioning model is based on ecological theories of interspecific relationships, competitive ability, and competitive exclusion principle and experimental designs

of both replacement and additive series. This new partitioning approach enables meaningful assessments of species interactions at both species and community levels and provides detailed insights into the mechanisms of species interactions that drive changes in ecosystem productivity. We believe that our framework, which is admittedly perfectible, is one promising avenue to determine effects of species interactions responsible for changes in ecosystem productivity, an approach that is long sought after in biodiversity–ecosystem productivity research (Loreau and Hector, 2019; Mahaut et al., 2020).

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Author contributions

R.M. and H.Y. designed the research; J.T., S.H. and R.M. generated growth and yield data with the GYPSY; and J.T., C.A.N., E.B.S., S.H., R.M., H.Y., G.T.F., C.V., and J.Z. contributed to the interpretations of the results and to the writing of the paper.

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Figure 1. Under the competitive hypothesis, more competitive species gain size (biomass or volume) and less competitive species lose size in mixture relative to their full density monocultures. The magnitude of competitive growth responses (i.e., proportional changes in individual size) increases with relative competitive ability (proportional deviations of species competitive ability from community average) from a minimum of 0 (at community average) to a maximum of $W_p/W_f - 1$ for more competitive species and -1 for less competitive species in competitive exclusion. The changes may not be linear, greater near community average and smaller with deviations of competitive ability (Gaudet & Keddy, 1988) or recourse availability (e.g., light, see Brüllhardt *et al*. 2020) away from community averages. W_f represents for individual size in full density monocultures and W_p represents for individual size in partial density monocultures.

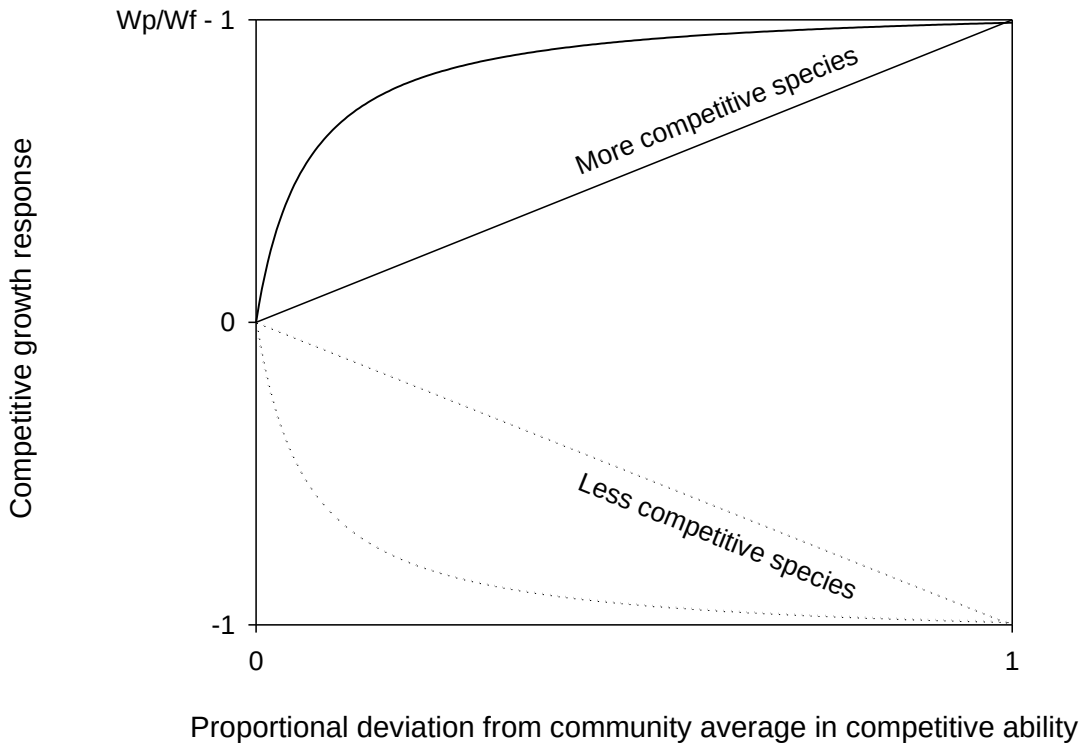

Figure 2. Partitioning net biodiversity effects (changes in stand volume in mixtures relative to monocultures) with competitive (a and b) and additive (c and d) partitioning models for 20- to 80-year-old mixed trembling aspen and white spruce with varying species compositions from nearly pure aspen (90% aspen) to nearly pure spruce (90% spruce) on average medium productivity sites in western Canada. The growth and yield data (***Table 1***) are generated with GYPSY (Huang et al., 2009) and calculations of biodiversity components with this figure are detailed in ***Table S1***.

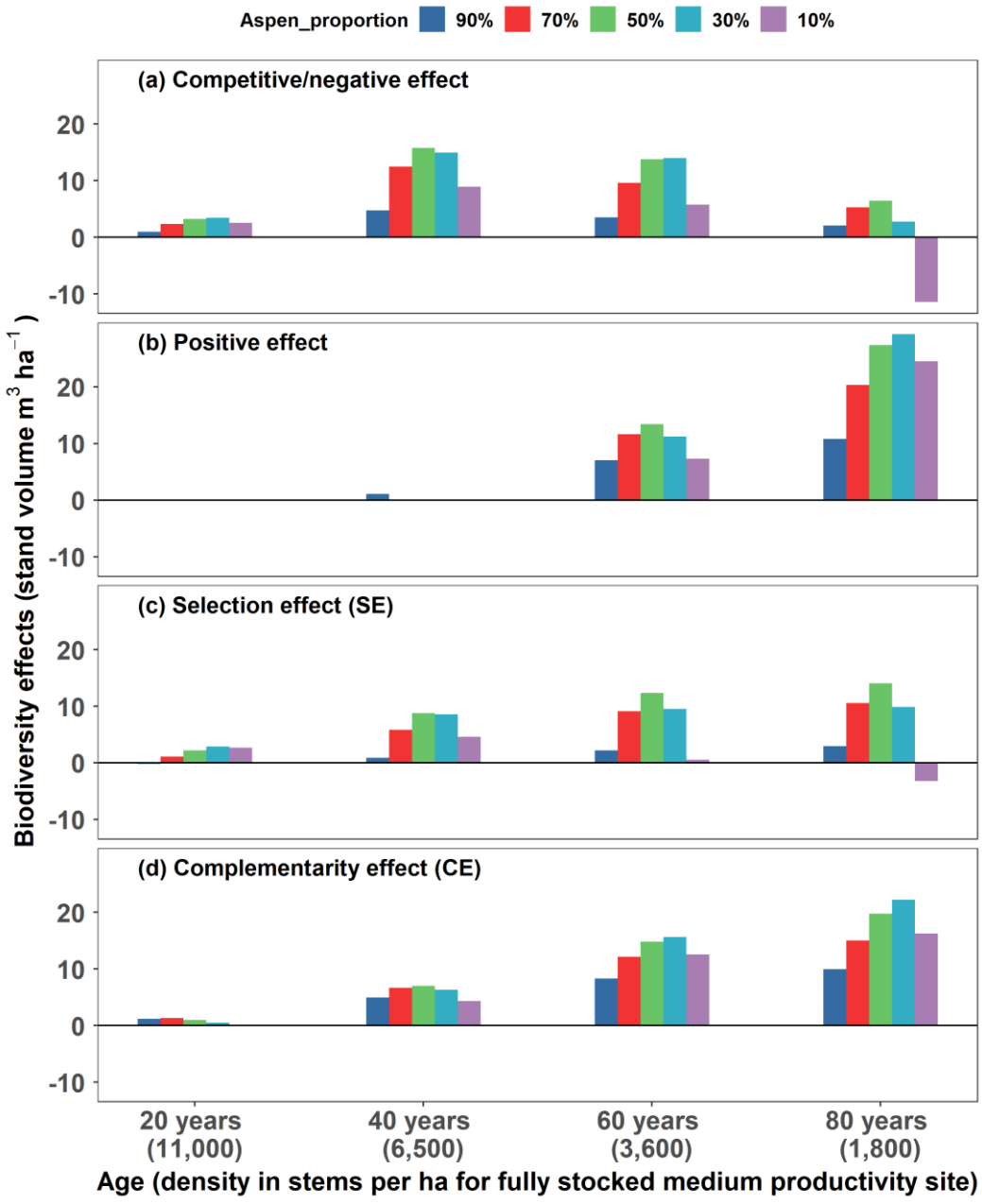

Table 1. Simulated and experimental species mixtures. BPM (biodiversity effects of partial density monocultures) are calculated from the differences between the partial density monoculture yield of more competitive species and total yield expected from species relative yields and full density monoculture yields (see competitive exclusion in ***Table S1*** and ***Table S2*** for detailed calculations).

Species mixture (species1:species2)	Age	Total density	Mixture composition		Full density monoculture yields		Observed yields in mixtures		Partial density monoculture yields		
			Species1	Species2	Species1	Species2	Species1	Species2	Species1	Species2	BPM
Simulated mixed trembling aspen and white spruce in western Canada generated with GYPSY model (Huang et al., 2009) (density and stand volume yield, stems and m^3 per hectare)											
Populus:Picea	20 years	11,000	0.9	0.1	23.7	0.7	22.3	0.1	23.3	0.5	1.9
Populus:Picea	20 years	11,000	0.7	0.3	23.7	0.7	19.0	0.2	22.5	0.6	5.7
Populus:Picea	20 years	11,000	0.5	0.5	23.7	0.7	15.1	0.3	21.4	0.6	9.2
Populus:Picea	20 years	11,000	0.3	0.7	23.7	0.7	10.6	0.4	19.8	0.7	12.2
Populus:Picea	20 years	11,000	0.1	0.9	23.7	0.7	5.0	0.5	16.9	0.7	13.9
Populus:Picea	40 years	3,600	0.9	0.1	110.4	27.2	104.5	3.4	108.3	15.5	6.3
Populus:Picea	40 years	3,600	0.7	0.3	110.4	27.2	90.3	7.6	103.5	20.7	18.1
Populus:Picea	40 years	3,600	0.5	0.5	110.4	27.2	72.4	12.1	97.0	23.4	28.2
Populus:Picea	40 years	3,600	0.3	0.7	110.4	27.2	49.6	17.5	87.4	25.3	35.2
Populus:Picea	40 years	3,600	0.1	0.9	110.4	27.2	20.6	23.9	70.6	26.7	35.1
Populus:Picea	60 years	1,800	0.9	0.1	189.7	88.3	180.5	9.6	186.1	47.0	6.6
Populus:Picea	60 years	1,800	0.7	0.3	189.7	88.3	158.1	22.4	177.3	64.3	18.0
Populus:Picea	60 years	1,800	0.5	0.5	189.7	88.3	128.1	38.1	164.8	73.7	25.8
Populus:Picea	60 years	1,800	0.3	0.7	189.7	88.3	85.4	58.5	144.8	80.5	26.1
Populus:Picea	60 years	1,800	0.1	0.9	189.7	88.3	28.6	83.0	109.2	85.9	10.8
Populus:Picea	80 years	1,100	0.9	0.1	240.2	143.1	229.6	13.7	235.6	73.3	5.1
Populus:Picea	80 years	1,100	0.7	0.3	240.2	143.1	203.7	33.0	224.1	102.0	13.1
Populus:Picea	80 years	1,100	0.5	0.5	240.2	143.1	167.3	58.2	207.6	117.8	15.9
Populus:Picea	80 years	1,100	0.3	0.7	240.2	143.1	110.3	94.0	179.1	129.4	6.8
Populus:Picea	80 years	1,100	0.1	0.9	240.2	143.1	26.2	139.6	124.5	138.9	-28.4

Experimental grassland mixtures (density and aboveground biomass yield, stems and grams per pot) (Mahaut et al., 2020)											
Bromus: Dactylis	13 weeks	6	0.5	0.5	5.5	9.8	2.6	8.6	5.3	11.5	3.8
Bromus: Lotus	13 weeks	6	0.5	0.5	5.5	6.3	3.8	3.2	5.3	4.7	-1.2
Bromus:Plantago	13 weeks	6	0.5	0.5	5.5	8.6	1.9	10.9	5.3	16.1	9.0
Bromus:Sanguisorba	13 weeks	6	0.5	0.5	5.5	4.4	2.9	2.2	5.3	3.6	0.3
Bromus:Trifolium	13 weeks	6	0.5	0.5	5.5	13.3	3.8	9.3	5.3	14.2	4.8
Dactylis:Lotus	13 weeks	6	0.5	0.5	9.8	6.3	11.8	2.0	11.5	4.7	3.4
Dactylis:Plantago	13 weeks	6	0.5	0.5	9.8	8.6	4.4	9.5	11.5	16.1	2.3
Dactylis:Sanguisorba	13 weeks	6	0.5	0.5	9.8	4.4	6.0	1.9	11.5	3.6	4.4
Dactylis:Trifolium	13 weeks	6	0.5	0.5	9.8	13.3	7.5	7.7	11.5	14.2	2.6
Lotus:Plantago	13 weeks	6	0.5	0.5	6.3	8.6	1.0	16.2	4.7	16.1	8.6
Lotus:Sanguisorba	13 weeks	6	0.5	0.5	6.3	4.4	1.9	2.6	4.7	3.6	-0.6
Lotus:Trifolium	13 weeks	6	0.5	0.5	6.3	13.3	2.4	9.2	4.7	14.2	4.4
Plantago:Sanguisorba	13 weeks	6	0.5	0.5	8.6	4.4	11.6	1.1	16.1	3.6	9.6
Plantago:Trifolium	13 weeks	6	0.5	0.5	8.6	13.3	10.2	6.9	16.1	14.2	3.3
Sanguisorba:Trifolium	13 weeks	6	0.5	0.5	4.4	13.3	1.9	13.4	3.6	14.2	5.3

Species codes: Populus - *Populus tremuloides*, Picea - *Picea glauca*, Bromus - *Bromus erectus*, Dactylis - *Dactylis glomerata*, Lotus - *Lotus corniculatus*, Plantago - *Plantago lanceolata*, Sanguisorba - *Sanguisorba minor*, and Trifolium - *Trifolium repens*.

Table 2. Partitioning net biodiversity effects (changes in aboveground biomass, g) with competitive and additive partitioning models using experimental data (***Table 1***) from a grassland diversity–productivity study (Mahaut et al., 2020). Calculations are detailed in ***Table S2***.

Species mixture	Competitive partitioning		Additive partitioning	
0.50Species1: 0.50Species2	Positive effect	Competitive/ negative effect	Complementarity effect (CE)	Selection effect (SE)
Bromus: Dactylis	1.8	1.7	2.7	0.9
Bromus: Lotus	1.2	-0.1	1.1	-0.1
Bromus:Plantago	2.5	3.2	4.3	1.4
Bromus:Sanguisorba	0.1	0.1	0.1	0.0
Bromus:Trifolium	0.9	2.8	3.6	0.0
Dactylis:Lotus	4.5	1.2	4.2	1.6
Dactylis:Plantago	4.3	0.3	5.1	-0.4
Dactylis:Sanguisorba	0.0	0.8	0.3	0.5
Dactylis:Trifolium	3.0	0.7	4.0	-0.3
Lotus:Plantago	7.6	2.3	7.9	1.9
Lotus:Sanguisorba	0.0	-0.9	-0.6	-0.3
Lotus:Trifolium	0.0	1.8	0.8	1.1
Plantago:Sanguisorba	1.5	4.7	3.9	2.3
Plantago:Trifolium	5.0	1.2	7.8	-1.6
Sanguisorba:Trifolium	2.9	3.6	3.9	2.6
Average	2.3	Competitive: 1.7 Negative: -0.2	3.3	0.6

Species codes: See ***Table 1***.