Title: Reducing 'sampling effect' in biodiversity effect estimation

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Abstract

Appropriate estimation of the effects of species interactions on ecosystem function is essential for understanding biodiversity effects and supporting development of environmental policies. Species undergo changes in competitive environment from monocultures to mixtures; highly productive species are generally more competitive and increase their performance and less productive species reduce their performance in mixtures, resulting in net increases of ecosystem function. This positive biodiversity effect, largely due to species differences in monoculture yield, does not involve complementary interactions (niche differentiation or facilitation) and therefore should not be included in biodiversity effect estimation. To reduce impacts of the 'sampling effect' and overestimation of biodiversity effects by additive biodiversity partitioning, we present a method to adjust species expected performance based on their monoculture performance and proportion in mixtures. Our method offers more appropriate estimations and interpretations of biodiversity effects for biodiversity experiments.

Keywords: null hypothesis, biodiversity effect, ecosystem function, complementarity

INTRODUCTION

Biodiversity affects ecosystem function (Cardinale *et al*. 2012; Isbell *et al.* 2017; Weisser *et al.* 2017; Yang *et al.* 2019). Positive biodiversity effects (enhanced ecosystem function) involve niche differentiation or facilitation (resource enhancement and positive abiotic/biotic feedbacks), resulting in some or all plant species thriving better in mixtures than what would be expected from monocultures (Vandermeer 1989; Hooper *et al*. 2005; Barry *et al* 2019). Negative effects (decreased ecosystem function) result from negative species interference, leading to reduced performance of species in mixtures relative to their monocultures (van der Heijden *et al*. 1999; Loreau 2000; Loreau & Hector 2001; Fox 2005; Barry *et al.* 2019). Distinguishing the effects of niche differentiation and facilitation is difficult and they are often collectively referred to as complementarity effects (Loreau *et al.* 2001; Loreau & Hector 2001; Forrester & Pretzsch 2015). Although positive biodiversity effects are desired for various purposes (Cardinale *et al*. 2012; Isbell *et al*. 2017), an appropriate estimation of the effects of species interactions on ecosystem function is essential; over- or under-estimation does not help understanding biodiversity effects and supporting development of environmental policies (Chu *et al*. 2019).

Various measures have been used to quantitatively assess the effects of biodiversity on ecosystem function. Direct biomass comparisons between mixtures and monocultures are criticized for ‘sampling effect’ where highly productive species that tend to dominate are likely to occur in high-diversity plant mixtures assembled randomly from a species pool (Aarssen 1997; Huston 1997; Tilman *et al*. 1997). The assessment of biodiversity effects on a relative yield basis (De Wit 1960; Harper 1977; Vandermeer 1989) eliminates sampling effect (Hector 1998; Wardle 1999), but provides no indications of interspecific interactions responsible for the observed ecosystem function changes (Loreau 1998; Wagg *et al*. 2019), a biodiversity effect that is more preferred from resource management perspective.

A more recent and popular approach defines a biodiversity effect as the net difference between observed yields and the yields expected from species proportions in mixtures and their monoculture yields (Loreau & Hector 2001). The sampling part of the 'sampling effect' is thought removed with such a balanced experimental design where all species in mixtures are compared relatively with their monocultures (Wardle 1999). As pointed out by Loreau & Hector (2001), however, the selection part of the 'sampling effect' still exists. Highly productive species are generally more competitive and more likely to increase their performances and less productive species reduce their performances in mixtures (Gaudet & Keddy 1988; Roscher & Schumacher 2016). The yield gain from more productive species overcompensates the loss from less productive species, resulting in net increases of mixture yields (Aarssen 1997; Huston 1997; Tilman *et al*. 1997; Wardle 1999; Wagg *et al.* 2019). It has been long debated whether such 'sampling effect' should be part of biodiversity effects (Hector 1998; Wardle 1999; Loreau 2000). Apparently, this positive biodiversity effect does not involve complementary interactions (Hector 1998; Loreau & Hector 2001) or strong interspecific competition (Hector 1998); instead, it comes from species competitive responses to intraspecific density changes from monocultures to mixtures and species differences in monoculture yield. Other than shifts in community functional composition towards more productive species (Hector 1998), the 'sampling effect' is not associated with enhanced resource availability or more efficient resource use and should not be part of positive biodiversity effects.

NULL EXPECTATION

Under a hypothetical scenario, species in mixtures perform exactly the same way as in monocultures, producing zero biodiversity effect (Loreau & Hector 2001; Fox 2005; Wagg *et al*. 2019). Testing the null hypothesis that species diversity does not affect ecosystem function is equivalent to testing if species in mixtures are competitively equivalent (Wagg *et al*. 2019), which would be valid only when species are functionally similar. Because of differences in monoculture yield, species are functionally different; more productive species are more competitive in resource acquisition and expected to have 'higher-than-expected' performance and less productive species to have 'lower-than-expected' performance in mixtures. The 'null expectation' therefore needs to be adjusted such that species in mixtures perform in a way of 'competitively equivalent'. A method to adjust species expected performance is outlined below.

$$\sum Y_{Ei} = \sum M_i RY_{Ei}[1 + RY_{Ei}(1 - RY_{Ei})\left(\frac{M_i}{\overline{M}} - 1\right)]$$

Where $RY_{Ei}$is expected relative yield (species proportion in mixture) and $(1 - RY_{Ei})$ represents additional resource availability due to lower density in mixtures relative to monocultures. Species competitive ability to utilize additional resource is assessed by their monoculture yield M_i relative to average monoculture yield $\overline{M}$; $\frac{M_i}{\overline{M}} > 1$ indicates above average competitive ability and therefore 'higher-than-expected' performance, $\frac{M_i}{\overline{M}} < 1$ indicates below average competitive ability and 'lower-than-expected' performance, and $\frac{M_i}{\overline{M}} = 1$ indicates average competitive ability and no change in expected performance. Thus, biodiversity effect would be the difference between sums of observed yields ($\sum Y_{Oi}$) and expected yields ($\sum Y_{Ei}$), or between positive (higher-than-expected) and negative (lower-than-expected) species responses to mixtures.

$$\sum Y_{Oi} - \sum Y_{Ei} = \begin{cases} > 0, & complementarity \\ = 0, & neutral \\ < 0, & interference \end{cases}$$

The dominant mechanism for observed biodiversity effects would be therefore self-explanatory.

DISCUSSION

Loreau & Hector (2001) separated their 'net biodiversity effect' into additive components called 'complementarity effect' and 'selection effect'. The mathematical derivation of the model is straightforward (covariance function), while the ecological interpretations of the additive components have been controversy (Carroll *et al.* 2011; Loreau *et al.* 2012; Pillai & Gouhier 2019; Wagg *et al*. 2019). The 'complementarity effect' represents species average responses from monocultures to mixtures, determined from species average relative yield change and average monoculture yield. The 'selection effect' measures individual species differences to the average response, not to their expected responses, and therefore is not equivalent to selection part of the 'sampling effect' as has been suggested (Loreau & Hector 2001; Fox 2005; Wagg *et al*. 2019). The 'selection effect' is positive if more productive species get higher-than-average performance or less productive species get lower-than-average performance, and negative when more productive species get lower-than-average performance or less productive species get higher-than-average performance (Loreau & Hector 2001). The interpretation of the additive partitioning has been focused on the positive sides of these two components (Loreau & Hector 2001; Wagg *et al*. 2019), whereas the ecological meanings of negative complementarity and selection effects are not clearly justified. Other than possible overestimation of biodiversity effect by 'net biodiversity effect' (Pillai & Gouhier 2019), the use of the word 'complementarity' that generally represents complementary interactions in ecology (Vandermeer 1989; Hooper *et* *al.* 2005; Barry *et al*. 2019) for species average response causes widespread confusion and misuse (Petchey 2003; Loreau *et al.* 2012; Barry *et al*. 2019). As a such, Petchey (2003) tried to redefine 'complementarity' to include all 'complementarity effect' values and to resolve the conflicts between ecological theories and additive biodiversity partitioning, which is apparently not successful.

The 'null expectation' adjustment raises the expected yields for more competitive species and lowers the expected yields for less competitive species, resulting in overall increases in expected performance of species mixtures and therefore decreases in the estimates of biodiversity effects. The level of adjustment increases with species differences in monoculture yield, but varies little with species proportion or relative yield (Fig. 1).

The need for 'null expectation' adjustment is minimal with similar among-species monoculture performances (Fig. 1). This may explain the long-term use of null hypothesis in agriculture and grassland experiments where species monoculture yields do not differ substantially (De Wit 1960; Harper 1977; Wagg *et al*. 2019). In woody plants and trees particular, among-species-differences in monoculture performance can be more than 10 times (Huang *et al*. 2018) and increase over time with accumulative growth of individuals (Wagg *et al*. 2019). Without competitive adjustment, detected 'biodiversity effect' would be meaningless if 'productive mixtures' are just more productive than monoculture average (Hector 1998). This is particularly true in forest industry where decision to go mixedwoods would be not justified if tree mixtures are more costly to establish and manage, but produce much less timber or biomass than highly productive monocultures, regardless of the level of 'net biodiversity effect' detected from 'null expectation'.

The 'null expectation' adjustment helps discern the ecological mechanisms responsible for changes in ecosystem function. Positive biodiversity effects can be attributed to generally higher-than-expected complementary interactions (Vandermeer 1989; Hooper *et al*. 2005; Barry *et al*. 2019) and negative biodiversity effects to lower-than-expected competitive suppression/species interferences (van der Heijden *et al*. 1999; Loreau 2000; Loreau & Hector 2001; Fox 2005; Barry *et al*. 2019), leaving a little room for misinterpretations. This is in contrast to additive biodiversity partitioning where the 'complementarity effect' has been largely used as indication of complementary interactions (Loreau *et al.* 2012; Barry *et al*. 2019), even though repeated warning against such a use (Loreau & Hector 2001, 2019; Petchey 2003; Fox 2005; Loreau *et al.* 2012; Barry *et al*. 2019; Wagg *et al.* 2019). The 'complementarity effect' adds little to the understanding of biodiversity-productivity relationships over 'net biodiversity effect', as the two terms share high similarity as would mathematical mean and weighted mean, and therefore are highly correlated (Ruijven & Berendse 2005; Fargione *et al*. 2007; Montès *et al*. 2008; Morin *et al*. 2011; Huang *et al.* 2018).

The values of competitive adjustment determined from a simple product of species abundance, resource availability, and relative monoculture yield seems reasonable according to the levels of 'net biodiversity effect' and 'selection effect' reported in mixed species experiments (Loreau & Hector 2001; Fargione *et al*. 2007; Huang *et al*. 2018). More accurate adjustment can be made by species-specific response to changes in density, resource availability, and competitive environment in mixtures.

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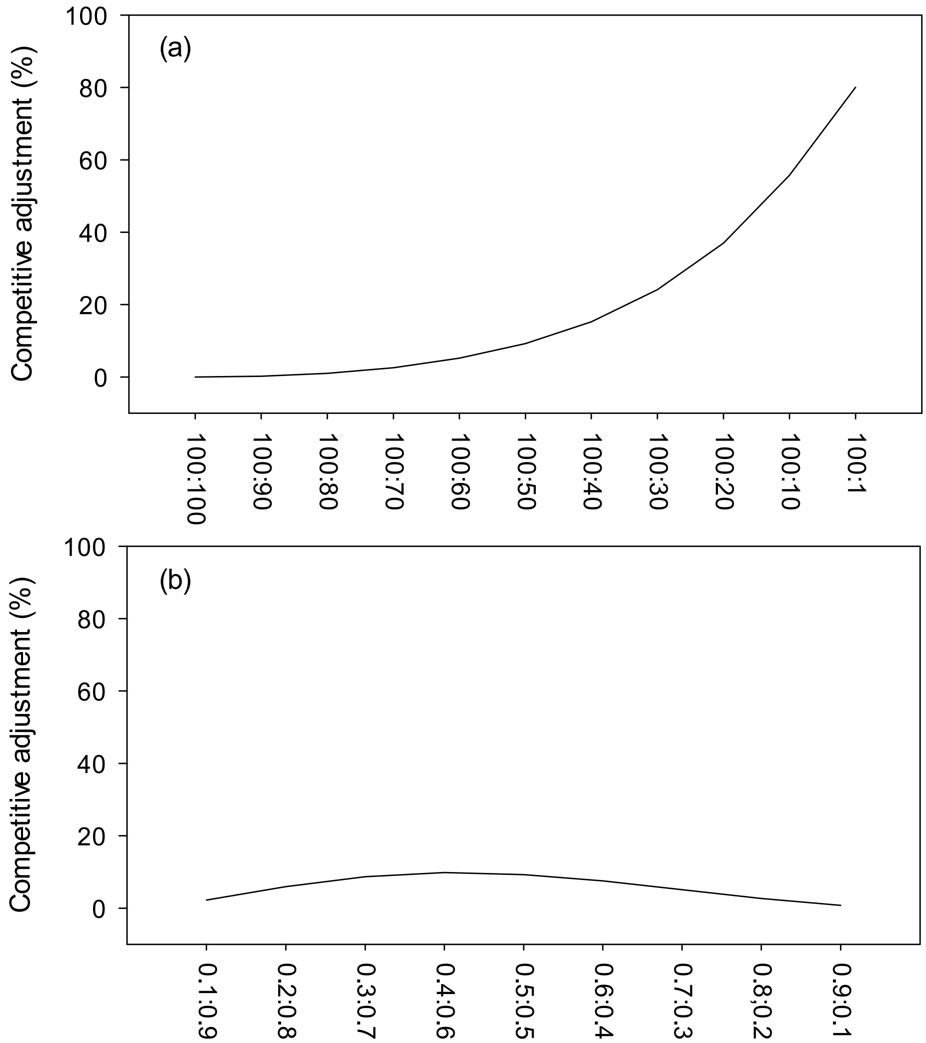

Fig. 1. Variations of competitive adjustment (relative to net biodiversity effect calculated as 30% of expected yields of two species) with (a) species differences in monoculture yield at fixed species proportions (0.50:0.50), and (b) species proportions at fixed monoculture yields (100:50) in hypothetical biodiversity experiments.