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METHOD

Partitioning the biodiversity effects on productivity into density and size components

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Abstract

Plant density and size — two factors that represent plant survival and growth — are key determinants of yield but have rarely been analysed explicitly in the context of biodiversity–productivity relationships. Here, we derive equations to partition the net, complementarity and selection effects of biodiversity into additive components that reflect diversity-induced changes in plant density and size. Applications of the new method to empirical datasets reveal contrasting ways in which plant density and size regulate yield in species mixtures. In an annual plant diversity experiment, overyielding is largely explained by selection effects associated with increased size of highly productive plant species. In a tree diversity experiment, the cause of overyielding shifts from enhanced growth in tree size to reduced mortality by complementary use of canopy space during stand development. These results highlight the capability of the new method to resolve crucial, yet understudied, demographic links between biodiversity and productivity.

KEYWORDS

biodiversity experiment, canopy packing, complementarity, ecosystem functioning, forest restoration, overyielding, plant diversity, primary productivity, species mixture, tree mortality

INTRODUCTION

Resolving the mechanisms by which multispecies mixtures produce greater biomass than monocultures has been of central interest to plant ecologists (Firbank & Watkinson, 1985; Hector et al., 1999; Tilman et al., 1996, 1997; Trenbath, 1974). The deviation of total biomass in a mixture from the average of its constituent species in monocultures is referred to as overyielding or the net biodiversity effect (Loreau & Hector, 2001; Trenbath, 1974; Vandermeer, 1989). Overyielding emerges because of diversity-induced changes in plant density (the number of plants per unit area, d) and/or plant size (the mean biomass per plant, w) (Marquard et al., 2009; Pretzsch & Forrester, 2017; Roscher et al., 2007), given the fact that total biomass equals dw. Plant density and size are key factors that represent two fundamental demographic processes — survival and growth. To date, however, we lack analytical methods to disentangle the two processes in biodiversity experiments that manipulate the number of species. Filling this gap between biodiversity–productivity relationships (Hector et al., 1999; Tilman et al., 1996; Trenbath, 1974) and density–size–yield relationships (Enquist et al., 1998; Harper, 1977; Yoda et al., 1963) can provide a common ground for finding optimal density and maximal yield in species mixtures.

Plant density and size can drive overyielding in multiple ways. Plant populations often undergo species-specific, self-thinning trajectories of density declines and mean size increments known as the Reineke's rule (Reineke, 1933), the −3/2 power law (Yoda et al., 1963), or related allometric scaling laws (Deng et al., 2012; Enquist et al., 1998). One-way overyielding can emerge is that the mixtures simply develop faster than monocultures along the same self-thinning trajectories (Pretzsch & Forrester, 2017). Alternatively, species mixing can shift the self-thinning trajectories themselves, allowing a greater number of plants with a given mean size to survive than in monocultures (Binkley, 1984; Pretzsch & Biber, 2016; Roscher et al., 2007; Urgoiti et al., 2023). Such shifts in density–size relationships indicate diversity-induced emergent properties that have been a significant subject of research in agriculture (Vandermeer, 1989) and forestry (Binkley, 1984; Pretzsch & Forrester, 2017) but have rarely been analysed explicitly in biodiversity experiments (Marquard et al., 2009; Roscher et al., 2007; Urgoiti et al., 2023).

In their seminal study, Loreau and Hector (2001) developed a method to partition the net biodiversity effect into complementarity and selection effects. The complementarity effect measures diversity-induced changes in the average relative yield associated with resource partitioning, facilitation or dilution effects while the selection effect reflects disproportionate dominance of a few highly productive species in species mixtures (Loreau & Hector, 2001; Tilman et al., 1997; van Ruijven et al., 2020). Using the partitioning method, subsequent experimental studies found cases in which complementarity effects are largely explained by increased plant size associated with enhanced resource-use efficiency in mixtures (Bu et al., 2017; van Ruijven & Berendse, 2003; Williams et al., 2017). Experiments manipulating the initial number of plants revealed density-dependent changes in the relative strengths of complementarity and selection effects (Polley et al., 2003; Stachová et al., 2013). These experiments provide evidence that complementarity and selection effects can both be affected by plant density and size. However, with existing analytical methods, we cannot quantify the independent roles of changes in density and size (i.e. survival and growth processes) during the course of community development. To disentangle the impacts of the two processes on complementarity and selection effects, a new method is needed.

Here, we develop an additive partitioning method to quantify the net, complementarity and selection effects of biodiversity that result from diversity-induced changes in plant density and size (Box 1, Figure 1). By applying the method to experimental datasets, we demonstrate its capability in discerning the survival and growth processes that underlie biodiversity–productivity relationships. We also show how the outcomes of this partition can provide new insights into density–size–yield relationships and discuss opportunities for future applications of the method.

METHODS

Complementarity and selection effects of biodiversity

Following Loreau and Hector (2001), we write N=Number of species in the mixture; M_i=Observed yield of species i in monocultures; $Y_{\mathrm{O},i}$=Observed yield of species i in the mixture; $Y_{\mathrm{E},i}=RY_{\mathrm{E},i}M_i$=Expected yield of species i in the mixture, defined as the product of the expected relative yield and the observed monoculture yield; $RY_{\mathrm{O},i}=Y_{\mathrm{O},i}\,/\,M_i$=Observed relative yield of species i in the mixture, defined as the ratio of the observed yield in the mixture to that in monocultures; $RY_{\mathrm{E},i}$=Expected relative yield of species i, defined as the proportion sown, planted, or inoculated (Loreau & Hector, 2001); and ΔRY_i=Difference between the observed and expected relative yields of species i.

It then follows that,

$$\Delta Y_i = Y_{\mathrm{O},i} - Y_{\mathrm{E},i} = \Delta RY_i M_i. \tag{1}$$

Here, ΔY_i is defined as the difference between the biomass of species i observed in the mixture and what is expected based on monoculture biomass. Loreau and Hector (2001) partitioned the net biodiversity effect $\Delta Y\ (=\sum_{i=1}^{N}\Delta Y_i)$ into complementarity and selection effects as follows:

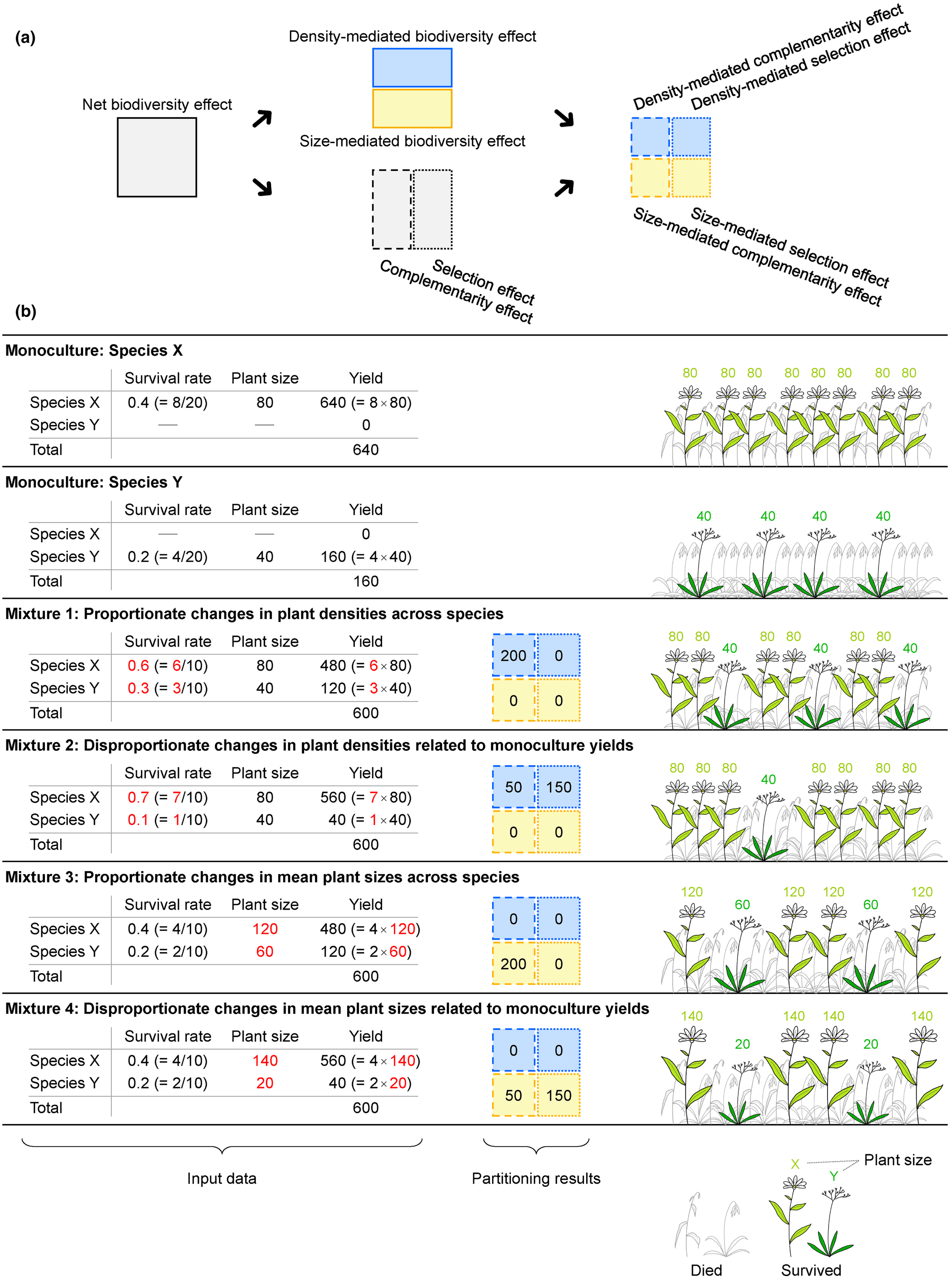
$$\Delta Y = \underbrace{N\overline{\Delta RY M}}_{\text{Complementarity effect}} + \underbrace{N\mathrm{cov}(\Delta RY, M)}_{\text{Selection effect}}. \tag{2}$$

Density- and size-mediated effects of biodiversity

We now partition the net biodiversity effect into density and size components (Box 1, Figure 1). By definition, the total biomass per unit area is given by the product of two values: plant density (the number of plants per unit area) and plant size (the mean biomass per plant). We partition the biodiversity effect by expressing it as a function of these two values. The partitioning approach follows that of Tatsumi et al. (2021, 2022) (see Supporting Text).

First, to quantify the biodiversity effect that results solely from changes in plant density, we define ΔD as the difference between the observed and expected plant densities (Box 1). Similar to the definition of the observed relative yield $RY_{\mathrm{O},i}$, we define the observed relative

FIGURE 1 Additive partitioning of net biodiversity effect into density- and size-mediated components. (a) Conceptual diagram of how net biodiversity effect can be partitioned into density- and size-mediated biodiversity effects (top), complementarity and selection effects (bottom), and their combinations (right). (b) Examples of density- and size-mediated complementarity and selection effects. All scenarios start with a plant density of 20 individuals. In monocultures, the yield of species X is 640 (= 8 individuals survived × mean plant size 80) and that of species Y is 160 (= 4 individuals survived × mean plant size 40). The expected yield in a 1:1 mixture is thus 400 (= [640 + 160]/2). Mixtures 1–4 describe scenarios in which the size of net diversity effect is the same ($\Delta Y = 200$) but for different reasons. The values shown in red indicate deviations from the expected final density (survival rate) or the expected mean plant size. In mixture 1, the survival rates of species X and Y increase proportionately by 50% the expected values; that is, from 0.4 in the monoculture to 0.6 in the mixture for species X and from 0.2 to 0.3 for species Y. In mixture 2, the survival rate of the high-yield species X increases by 75% while that of the low-yield species Y decreases by 50%. In mixture 3, the mean plant sizes of species X and Y increase proportionately by 50%. In mixture 4, the mean plant size of the high-yield species X increases by 75% while that of the low-yield species Y decreases by 50%.



Monoculture: Species X

	Survival rate	Plant size	Yield
Species X	0.4 (= 8/20)	80	640 (= 8 × 80)
Species Y	—	—	0
Total			640

Monoculture: Species Y

	Survival rate	Plant size	Yield
Species X	—	—	0
Species Y	0.2 (= 4/20)	40	160 (= 4 × 40)
Total			160

Mixture 1: Proportionate changes in plant densities across species

	Survival rate	Plant size	Yield
Species X	0.6 (= 6/10)	80	480 (= 6 × 80)
Species Y	0.3 (= 3/10)	40	120 (= 3 × 40)
Total			600

200	0
0	0

Mixture 2: Disproportionate changes in plant densities related to monoculture yields

	Survival rate	Plant size	Yield
Species X	0.7 (= 7/10)	80	560 (= 7 × 80)
Species Y	0.1 (= 1/10)	40	40 (= 1 × 40)
Total			600

50	150
0	0

Mixture 3: Proportionate changes in mean plant sizes across species

	Survival rate	Plant size	Yield
Species X	0.4 (= 4/10)	120	480 (= 4 × 120)
Species Y	0.2 (= 2/10)	60	120 (= 2 × 60)
Total			600

0	0
200	0

Mixture 4: Disproportionate changes in mean plant sizes related to monoculture yields

	Survival rate	Plant size	Yield
Species X	0.4 (= 4/10)	140	560 (= 4 × 140)
Species Y	0.2 (= 2/10)	20	40 (= 2 × 20)
Total			600

0	0
50	150

density as $RD_{\mathrm{O},i} = D_{\mathrm{O},i} / D'_i$, where $D_{\mathrm{O},i}$ and D'_i denote the observed density of species i in the mixture and monocultures, respectively. We also define the expected relative density $RD_{\mathrm{E},i}$ as the proportion of species i sown, planted or inoculated in the mixture (i.e. $RD_{\mathrm{E},i} = RY_{\mathrm{E},i}$).

We write ΔRD_i for the difference between the observed and expected relative densities of species i. The deviation ΔD of species i then reads

$$\Delta D_i = D_{\mathrm{O},i} - D_{\mathrm{E},i} = \Delta RD_i D'_i. \tag{3}$$

BOX 1 Partitioning net biodiversity effect into density- and size-mediated components

Partitioning equation

We define plant density as the number of plants per unit area and plant size as the mean biomass per plant (Firbank & Watkinson, 1985; Harper, 1977; Shinozaki & Kira, 1956). Net biodiversity effect ΔY can be partitioned into density- and size-mediated complementarity and selection effects (Figure 1a). A positive density-mediated complementarity effect indicates proportionate increases in plant densities across species (Mixture 1 in Figure 1b). A positive density-mediated selection effect suggests disproportionate increases in plant densities of high-yield species (Mixture 2 in Figure 1b). A positive size-mediated complementarity effect indicates proportionate increases in mean plant sizes across species (Mixture 3 in Figure 1b). A positive size-mediated selection effect suggests disproportionate increases in mean plant sizes of high-yield species (Mixture 4 in Figure 1b). The four components can also take negative values; for example, a negative size-mediated selection effect indicates disproportionate decreases in plant sizes of high-yield species.

The additive partitioning equation of the four components reads

$$\begin{aligned}\Delta Y = {} & \underbrace{\sum_{i=1}^{N} \frac{\overline{M}}{2M_i}\left(W_{\mathrm{O},i}+W_{\mathrm{E},i}\right)\Delta D_i}_{\text{Density-mediated complementarity effect}} + \underbrace{\sum_{i=1}^{N}\left(\frac{M_i-\overline{M}}{2M_i}\right)\left(W_{\mathrm{O},i}+W_{\mathrm{E},i}\right)\Delta D_i}_{\text{Density-mediated selection effect}} \\ & + \underbrace{\sum_{i=1}^{N} \frac{\overline{M}}{2M_i}\left(D_{\mathrm{O},i}+D_{\mathrm{E},i}\right)\Delta W_i}_{\text{Size-mediated complementarity effect}} + \underbrace{\sum_{i=1}^{N}\left(\frac{M_i-\overline{M}}{2M_i}\right)\left(D_{\mathrm{O},i}+D_{\mathrm{E},i}\right)\Delta W_i}_{\text{Size-mediated selection effect}},\end{aligned} \tag{B1.1}$$

where the variables are defined as follows: N=Number of species in the mixture; M_i = Observed yield of species i in monocultures; $D_{\mathrm{O},i}$ = Observed plant density of species i in the mixture; $D_{\mathrm{E},i}$ = Expected plant density of species i in the mixture, defined as the product of the expected relative density (i.e. the proportion sown, planted or inoculated) and the observed monoculture density of species i; ΔD_i = Difference between the observed and expected plant densities of species i; $W_{\mathrm{O},i}$ = Observed mean per-plant biomass of species i in the mixture; $W_{\mathrm{E},i}$ = Expected mean per-plant biomass of species i in the mixture, defined as its mean plant size in monocultures; and ΔW_i = Difference between the observed and expected mean per-plant biomass of species i.

Note that Equation B1.1 can be extended to partition the density-mediated effects further into germination-mediated effects and post-germination density-mediated effects (see Supporting Text).

Data requirements

The partitioning method is applicable to any biodiversity experiments (but not observational studies) in which plant species (e.g. herbs, trees, algae) are grown in respective monocultures and mixtures. The specific data required are: (i) the initial density of each species sown, planted, or inoculated in each experimental unit (e.g. plot, chemostat); (ii) the biomass y of each species in each unit; and (iii) the plant density d of each species in each unit at the time of biomass measurement. Optionally, (iv) the density of germinated seeds can be used to quantify the germination-mediated effects. Note that the biomass y does not have to be recorded at the individual level but only at the species level. Plant density d can be measured either by counting the individuals directly or by dividing the species biomass y by the mean per-plant biomass of representative individuals in each sampling unit (Marquard et al., 2009).

R package

The partitioning method can be implemented using the R (R Core Team, 2023) package `'densize'` (DENSIty and SIZE) available at GihHub (https://github.com/communityecologist/densize).

Importantly, ΔD_i serves as the density-analogue to ΔY_i (Equation 1) that does not account for plant size.

Next, to quantify the biodiversity effect associated with changes in plant size, we write $W_{\mathrm{O},i}$ for the mean plant size of species i observed in the mixture (Box 1). We define the expected mean plant size of species i as its mean plant size in monocultures (i.e. $W_{\mathrm{E},i} = W_i'$). The difference between the observed and expected plant sizes of species i then reads

$$\Delta W_i = W_{\mathrm{O},i} - W_{\mathrm{E},i} = W_{\mathrm{O},i} - W_i'. \tag{4}$$

Because the biomass per unit area is given by the product of plant density and size, the difference in the observed and expected biomass can be expressed as

$$\Delta Y_i = D_{\mathrm{O},i} W_{\mathrm{O},i} - D_{\mathrm{E},i} W_{\mathrm{E},i}. \tag{5}$$

By combining Equations 3–5, the net biodiversity effect can be expressed as a function of changes in plant density ΔD_i and plant size ΔW_i that result from species mixing (see Supporting Text for derivation):

$$\Delta Y = \underbrace{\sum_{i=1}^{N} \frac{1}{2}\left(W_{\mathrm{O},i} + W_{\mathrm{E},i}\right)\Delta D_i}_{\text{Density – mediated biodiversity effect}} + \underbrace{\sum_{i=1}^{N} \frac{1}{2}\left(D_{\mathrm{O},i} + D_{\mathrm{E},i}\right)\Delta W_i}_{\text{Size – mediated biodiversity effect}}. \tag{6}$$

The complementarity and selection effects (Equation 2) can also be expressed as functions of ΔD_i and ΔW_i (see Supporting Text). Consequently, the net biodiversity effect is partitioned into four components as shown in Equation B1.1 (Box 1).

Germination-mediated effect of biodiversity

Equations B1.1 and 6 can be extended to partition the density-mediated biodiversity effect further into germination-mediated biodiversity effect and post-germination density-mediated biodiversity effect (see Supporting Text for derivation) (Figure S1). Biodiversity experiments using herbaceous plants are typically initiated by sowing seeds (Hector et al., 1999). The seeds can vary in their germination rates owing to intra- and interspecific interactions among neighbouring seeds (Bergelson & Perry, 1989; Tielbörger & Prasse, 2009). Partitioning of the germination-mediated effects allows quantifications of over- or under-yielding caused by such diversity-induced variation in germination rates. Note that the germination-mediated effects are irrelevant for experiments initiated by planting young individuals which is mostly the case for tree diversity experiments (Grossman et al., 2018).

Species-level partitioning

Quantifying the net biodiversity effect for each species can help elucidate the links between mixture yield and the morphological and physiological traits of the constituent species (Isbell et al., 2011; Marquard et al., 2009; Roscher et al., 2007). Equations B1.1 and 6 can partition the net biodiversity effect at the species-level by calculating each term for species $i = 1, 2, \ldots, N$ separately. For example, suppose a 1:1 mixture in which the density of species X increases by 50% and that of species Y decreases by 50% while all else remains the same between the two species and between the mixture and monocultures. In such a case, the species-level density-mediated effects of species X and Y will take positive and negative values with the same absolute size, respectively, while the community-level density-mediated effect will add up to 0.

Theoretical model

To verify the performance of the partitioning method, we conducted sensitivity analyses using a theoretical model (see Supporting Text and Table S1 for details). Briefly, we built on a multi-species competition model developed by Firbank and Watkinson (1985) to explicitly simulate plant density, mean per-plant biomass and seedling emergence under different strengths of interspecific competition associated with survival (α_{ij}), size increment (β_{ij}) and germination (γ_{ij}). The analyses showed that the density-, size- and germination-mediated biodiversity effects responded to the corresponding types of competition α_{ij}, β_{ij} and γ_{ij} (Figure S2), confirming the validity of the partitioning method.

APPLICATIONS

Annual plant diversity experiment

We first applied the partitioning method to a biodiversity experiment using annual plants. Five herbaceous species (*Arthraxon hispidus*, *Bidens pilosa*, *Digitaria ciliaris*, *Kummerowia stipulacea* and *Persicaria longiseta*) were sown solely or in mixtures of two, three or four species. In addition to the number of species, the initial density was manipulated by sowing either a total of 24 or 72 seeds per pot. We counted the number of emerged seedlings after 2 weeks of sowing when true leaves started to develop. After a growing season, plants were harvested, dried and weighed. Using the density and yield data, we calculated the net biodiversity effects and their components (see Table S2 and Supporting Text for details).

Tree diversity experiment

We next analysed a tree-census dataset collected in a tree diversity experiment. The experiment consisted of Sakhalin fir (*Abies sachalinensis*), monarch birch (*Betula *maximowicziana*) and Japanese oak (*Quercus crispula*) planted solely or in a mixture. We calculated the net biodiversity effects and their components after 1, 2, 3, 16 and 31 years of planting (see Supporting Text and Tatsumi (2020) for details).

RESULTS AND DISCUSSION

Annual plant diversity experiment

Applications of the partitioning method to the annual plant diversity experiment identified contrasting roles of plant density and size in driving biodiversity–productivity relationships (Figure 2). Total biomass increased with species richness regardless of the initial seed densities (Figure 2a). The positive net biodiversity effects (Figure 2b) were explained by a combination of negative density-mediated effects (Figure 2c) and positive size-mediated effects (Figure 2f). The opposite signs of density- and size-mediated biodiversity effects on overyielding suggest trade-offs between survival and growth. Previous biodiversity experiments have also found positive impacts of species mixing on either plant density (Marquard et al., 2009; Roscher et al., 2007) or size (Huang et al., 2018; Potvin & Gotelli, 2008; van Ruijven & Berendse, 2003; Williams et al., 2017) but not necessarily both (Grossman

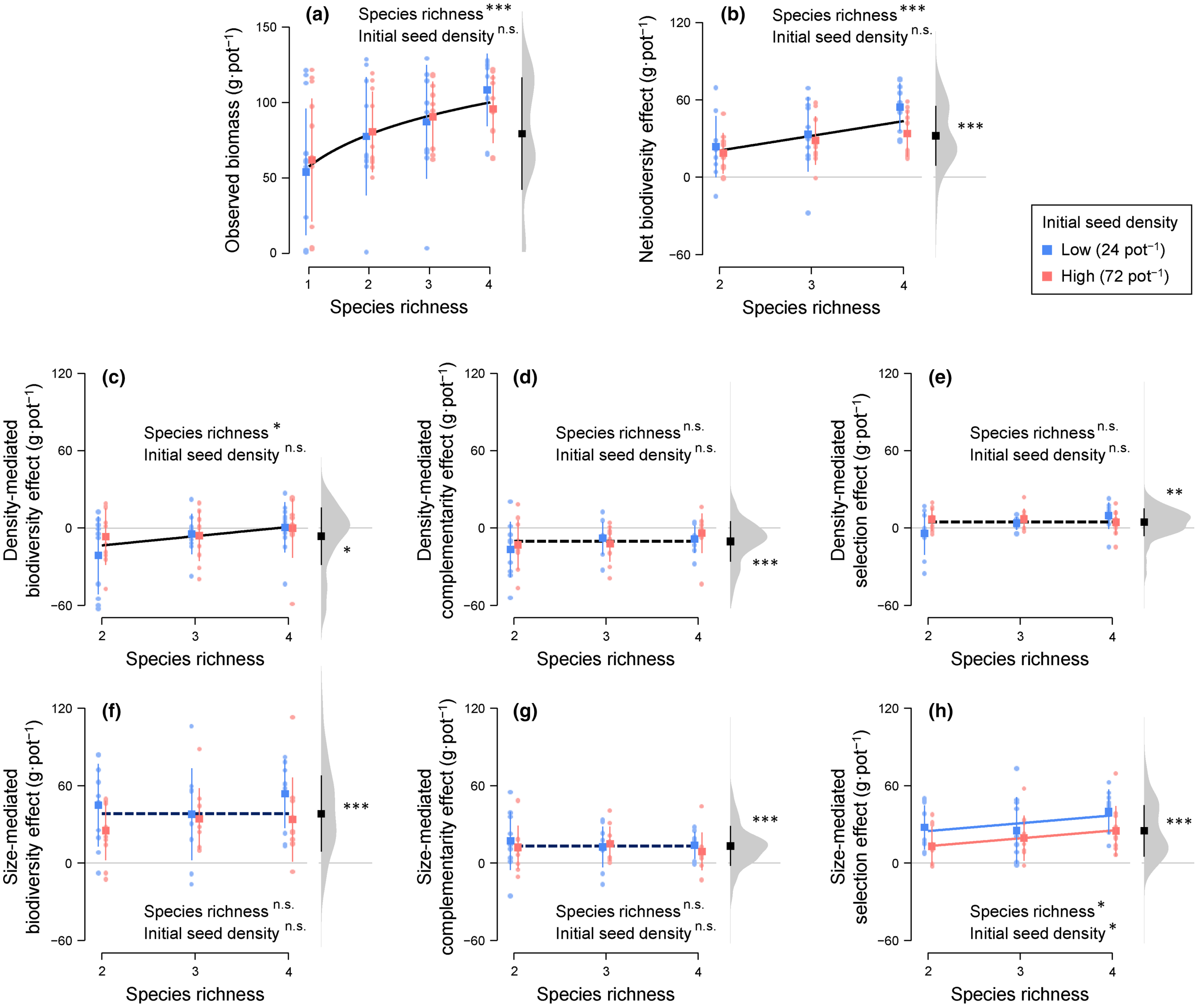


FIGURE 2 Observed biomass, net biodiversity effect and components of net biodiversity effect in an annual plant diversity experiment. (a) Observed biomass, (b) net biodiversity effect and (c–h) its components as functions of species richness ($n = 90$). Squares and vertical bars show the means and standard deviations, respectively. Solid ($p < 0.05$) and dashed ($p \geq 0.05$) lines indicate the impacts of species richness. Density curves represent Gaussian kernel density estimates. One-sample *t*-test was used to test the deviations of mean values from 0. Statistical significance: n.s. (not significant), $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Note that: Net biodiversity effect = Density-mediated biodiversity effect + Size-mediated biodiversity effect = Density-mediated complementarity effect + Density-mediated selection effect + Size-mediated complementarity effect + Size-mediated selection effect.

et al., 2018). Nevertheless, it is worth noting that, in the current experiment, the negative density-mediated biodiversity effects approached 0 with increasing species richness (Figure 2c), suggesting enhanced plant growth without compensatory mortality.

The negative density-mediated biodiversity effects (Figure 2c) were attributed to reductions in germination rates rather than post-germination survival rates (Figure S3) according to the partitioning of germination- and post-germination density components (see Methods and Supporting Text). Previous studies have shown evidence for germination inhibition among heterospecific seeds associated with ecophysiological processes such as allelopathic effects and resource preemption (Bergelson & Perry, 1989; Tielbörger & Prasse, 2009). In the current experiment, such negative interspecific seed interactions were found to be attenuated by increasing species richness (Figure S3a). Once germinated, plants in mixtures survived as much as those in monocultures (Figure S3d). These results underscore the relevance of diversity-dependent germination as a critical process in driving biodiversity–productivity relationships.

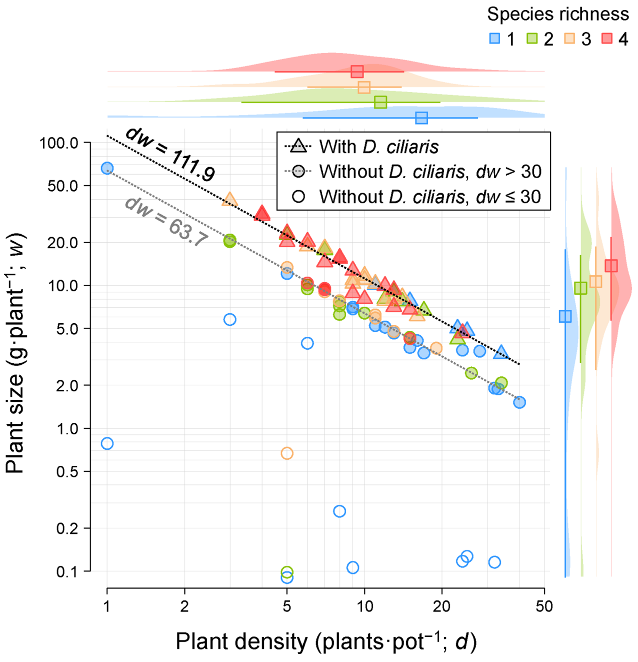


FIGURE 3 Density–size relationships in an annual plant diversity experiment. Relationships between plant density (number of plants per pot) and plant size (mean biomass per plant). Each dotted line shows the combination of density (d) and size (w) with a constant yield (y) such that $dw = y$ (i.e. slope $= -1$ on the log–log scale). The black and grey dotted lines represent the mean yield of pots with *Digitaria ciliaris* and the rest of the pots with total yield $dw > 30$g dry mass, respectively. Squares, bars and density curves show the means, standard deviations and sample distributions, respectively. Plant density decreased (top margin, $p < 0.001$) while plant size increased (right margin, $p < 0.01$) with species richness (tested based on the Pearson's product moment correlation coefficients).

Total biomass showed two distinct endpoints (Figure 3) depending on whether the most productive species *D. ciliaris* was present or not in the community (Figure S4). Plant density declines were offset by plant size increments within each group of communities (slopes = −1 on Figure 3), following the law of constant final yield typically found in plant populations (Shinozaki & Kira, 1956; Weiner & Freckleton, 2010). Most communities fell on either of the two lines representing constant yield, except for some outliers that had low plant densities or sizes (Figure 3) potentially due to uncontrolled factors (e.g. pathogens). Greater species richness increased the chance of communities to switch from the bottom line to the upper line on the density–size diagram (Figure 3). This density–size pattern coincides with the outcome of the partitioning method, which showed positive selection effects (Figure 2e,h) indicating disproportionate contributions of highly productive species to overyielding (Loreau & Hector, 2001). The positive impacts of species richness on final yields (Figure 3) and size-mediated selection effects (Figure 2h) collectively suggest enhanced per-plant growth of *D. ciliaris* under interspecific interactions.

Tree diversity experiment

The partitioning method revealed temporal changes in density- and size-mediated components of biodiversity effects in the tree diversity experiment (Figure 4). The net biodiversity effect was positive and increased with time (Figure 4a). This positive net biodiversity effect was due to enhanced tree size in the mixture during early years and increased tree density later on (Figure 4a). The density–size diagram showed an initial phase of size increments without density declines and subsequent self-thinning stages that followed the −3/2 power law (Yoda et al., 1963) (Figure 5a). These results agree well with previous findings that species mixing often promotes tree growth via canopy packing in young forests (Binkley et al., 2003; Potvin & Gotelli, 2008; Williams et al., 2017) while mortality plays minor roles early on (Grossman et al., 2018; Huang et al., 2018). Species-level partitioning showed that the positive size-mediated biodiversity effects in the first few years were largely driven by enhanced growth of early- and mid-successional species (*B. maximowicziana* and *Q. crispula*) (Figure 5b; Table S3). The complementarity and selection effects increased positively and negatively with stand age, respectively (Figure 4b).

Over the course of stand development, there was an increasing trend in density-mediated complementarity effect (Figure 4c) attributed to alleviation of self-thinning by vertical stratification in the mixture (Tatsumi, 2020). The mixture allowed greater numbers of trees with a given mean size to survive, thereby

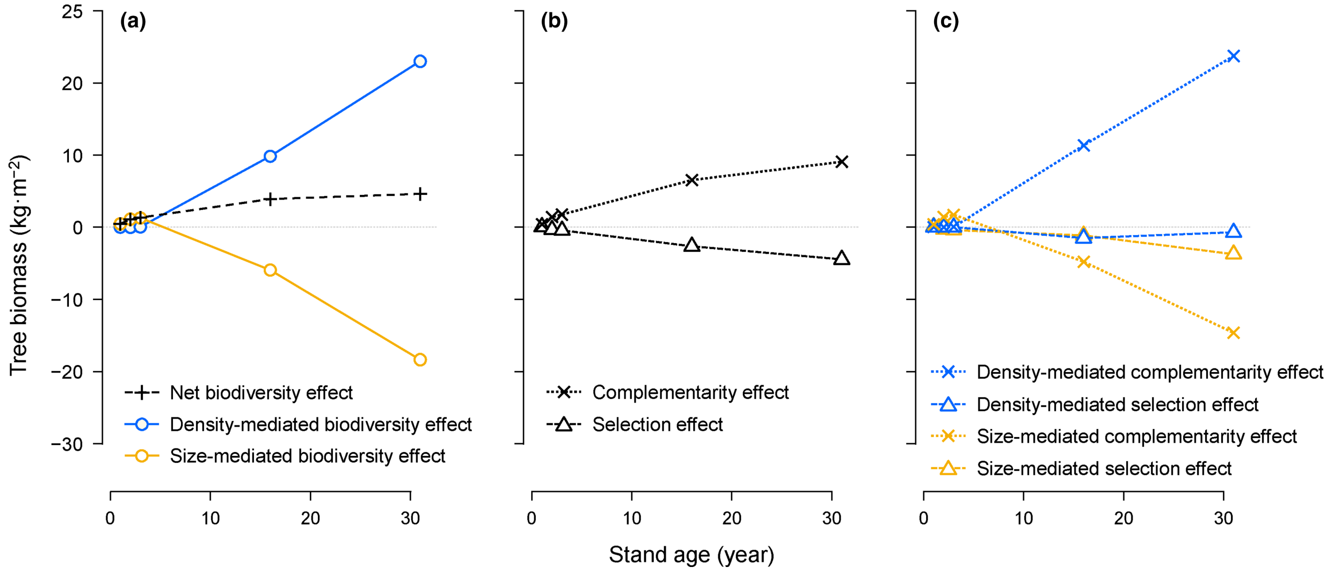


FIGURE 4 Net biodiversity effect and its components in a tree diversity experiment. (a) Net biodiversity effect and density- and size-mediated biodiversity effects as functions of stand age. (b) Complementarity and selection effects as functions of stand age. (c) Density- and size-mediated complementarity and selection effects as functions of stand age. Note that: Net biodiversity effect = Density-mediated biodiversity effect + Size-mediated biodiversity effect = Complementarity effect + Selection effect = Density-mediated complementarity effect + Density-mediated selection effect + Size-mediated complementarity effect + Size-mediated selection effect.

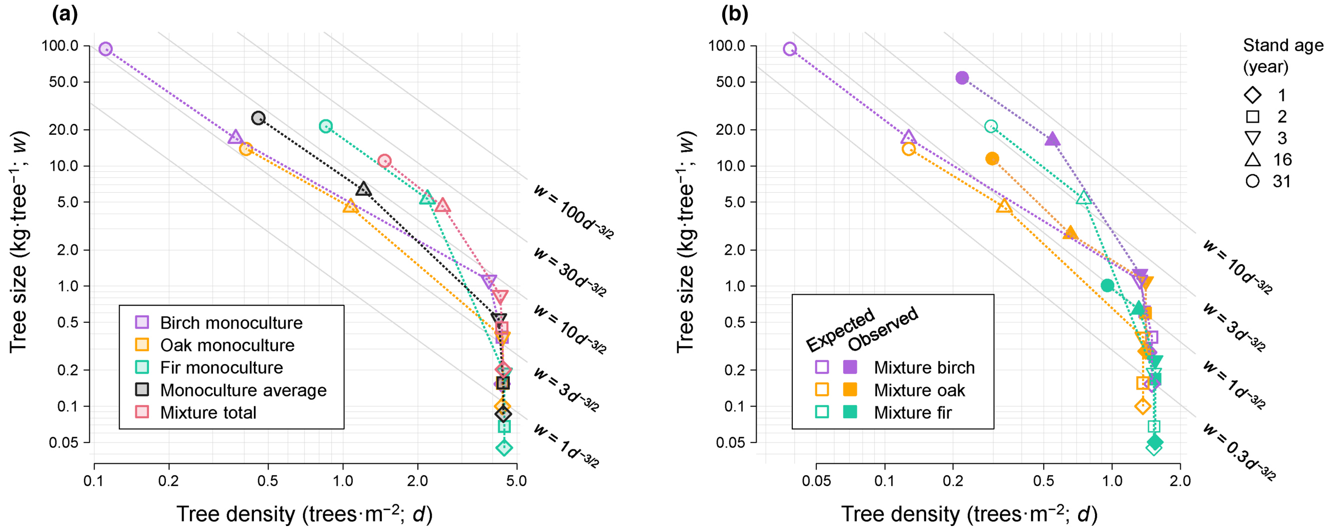


FIGURE 5 Density–size relationships in a tree diversity experiment. (a) Relationships between tree density (number of trees per m^2) and tree size (mean aboveground biomass per tree) at the stand level. Diagonal lines show examples of possible thinning trajectories along which tree size (w) increases in response to decreasing tree density (d) to the power of $-3/2$. (b) Expected and observed tree densities and sizes for each of the three species in the mixture stand. The expected densities and sizes are based on their values in monocultures.

pursuing an upper-right trajectory on the density–size diagram (Figure 5a). The increasing density-mediated complementarity effect (Figure 4c) reflects the fact that higher tree densities were observed in the mixture than expected for all the three constituent species (Figure 5b). Our partition further showed that the size-mediated complementarity and selection effects increased negatively with time (Figure 4c). This temporal pattern was explained by the suppressed growth of highly productive, late-successional species (*A. sachalinensis*) being overtopped by other species in the mixture (Figure 5b; Figure S5). Overall, these results highlight the capability of the partitioning method to disentangle the survival and growth processes by which species mixing enhances forest productivity.

Future applications

The new partitioning method provides a powerful means to discern the roles of plant density and size in biodiversity experiments that manipulate the number of species (Grossman et al., 2018; Hector et al., 1999; Tilman et al., 1996). Central to our method is that it can be applied post hoc to biodiversity experiments, including those that are already being conducted, without manipulating any factors other than species richness. The only data required, besides what is needed to calculate the net biodiversity effect sensu Loreau and Hector (2001), is plant density (Box 1, Figure 1). Plant density can be measured either by counting the individuals directly or by dividing species biomass by mean per-plant biomass (Marquard et al., 2009).

Using the partitioning method proposed by Loreau and Hector (2001), previous studies have found temporal shifts in net biodiversity effects from selection to complementary via mechanisms such as plant–soil feedback (Cardinale et al., 2007; Fargione et al., 2007; Reich et al., 2012), character displacement (Zuppinger-Dingley et al., 2014) and structural development (Feng et al., 2022; Huang et al., 2018). Using our new method, we found significant size-mediated effects in the short term (Figure 2f) and density-mediated effects in the long term (Figure 4a). A promising way forward would be to verify the generality and mechanisms of these temporal shifts from size- to density-mediated effects of biodiversity. The interlinkages between the components of net biodiversity effects and density–size patterns (e.g. constant final yield, −3/2 power law; Figures 3 and 5) also warrant future investigation.

Our method is capable of partitioning net biodiversity effects into species-level components. The estimated contributions of individual species to the overall mixture yield can be used in downstream analyses to explore their links to functional traits. In our tree diversity experiment, species greatly differed in their density- and size-mediated biodiversity effects (Table S3), implying trait-mediated growth–survival trade-offs. For example, *B. maximowicziana*, characterized by thin leaves associated with fast growth in light but limited survival in shade (Koike, 1986), showed positive density-mediated biodiversity effects (Table S3). This result can be explained by the species' fast-growing strategy, which allowed them to overtop other species in the mixture, leading to increased chances of survival. While post hoc partitioning methods, including ours and Loreau and Hector's (2001), are essentially phenomenological, analysing the links between species-level components and traits can provide insights into lower-level processes (i.e. specific mechanisms such as resource partitioning or facilitation) that generate higher-level phenomena (complementarity and selection effects) (Loreau et al., 2012).

The last two decades have witnessed significant accumulation of data on plant density and size in biodiversity experiments (Marquard et al., 2009; Roscher et al., 2007; Stachová et al., 2013) fuelled by the growing number of tree diversity experiments (Binkley et al., 2003; Grossman et al., 2018; Paquette et al., 2018; Tatsumi, 2020; Williams et al., 2017). With the increasing availability of data, our new method can help ecologists reveal survival and growth processes in species mixtures. Moving forward, open questions include determining the magnitude of density- and size-mediated biodiversity effects across (1) different taxonomic and functional groups, (2) environmental gradients and (3) planting designs and thinning operations. Answering these questions can have important implications for optimal density management in mixed-species forestry, restoration and intercropping systems across different environments.

A key benefit of the new method is that it quantifies the density and size components in the same unit as the net biodiversity effect (e.g. biomass per unit area), allowing straightforward comparisons between the effects of plant density and size on yield (Figures 2 and 4). Plant density and size have been a subject of intensive research in plant population ecology (Enquist et al., 1998; Harper, 1977; Yoda et al., 1963), agriculture (Deng et al., 2012; Vandermeer, 1989), and forestry (Binkley, 1984; Pretzsch & Forrester, 2017; Reineke, 1933), but have received limited attention in biodiversity–productivity research (Marquard et al., 2009; Roscher et al., 2007; Urgoiti et al., 2023). Empirical applications of the new method demonstrate how density–size patterns, such as constant final yield typically found in monocultures (Shinozaki & Kira, 1956; Weiner & Freckleton, 2010), can provide a new perspective to overyielding in mixtures. Our findings highlight the capability of the method to bridge the existing gap between classic density–size relationships and biodiversity–productivity relationships. Bridging this gap can help uncover survival–growth dynamics in species mixtures, making biodiversity–productivity research more predictive and relevant to non-experimental natural ecosystems.

AUTHOR CONTRIBUTIONS

Shinichi Tatsumi conceived the idea, developed the methods, collected and compiled the data and conducted the analyses. Shinichi Tatsumi and Michel Loreau wrote and revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The annual -plant diversity experiment dataset and the tree diversity experiment dataset are available at Figsahre (doi: 10.6084/m9.figshare.23796381 and 10.6084/m9.figshare.23796363). The R code used for the analyses is included as part of the 'densize' package available at Github (https://github.com/communityecologist/densize).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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