

Research

Reconsidering the Price equation: a new partitioning based on species abundances and trait expression

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Understanding the causes of the generally positive relationship between biodiversity and ecosystem function (BEF) is a major research focus in ecology. Early analyses of BEF used a modification of the evolutionary Price equation to partition effects of biodiversity into components of complementarity (species richness) and dominance (species composition). However, early experiments and data on BEF did not use information on species traits or relative abundances. Here we extend the Price partition of the total expression of a single trait (such as leaf area) between two communities into five additive components: 1) species richness; 2) average species trait expression; 3) relative abundance; 4) the combined effects of relative abundance and trait expression; 5) absolute abundance. When applied to presence–absence data with no trait variation, the method yields a result that is identical to the original Price partition into two components of complementarity and dominance. When applied to an analysis of relative abundance itself as a trait, our method quantifies the strength of species co-occurrences as a difference in Simpson diversity between the communities. We tested the new partition with artificial data sets and null model comparisons, and applied it to a long-term data set on plant succession. A key finding is that the effects of total abundance might be very important when comparing two communities, and possibly could account for results from previous studies in which complementarity emerged as an important contributor to BEF.

Keywords: functional traits, plant community assembly, Price equation, succession, variance partitioning

Introduction

The relationship between biodiversity and ecosystem function has been a key research focus for over 30 years (Loreau et al. 2002, Tilman et al. 2014, Clark et al. 2019, Jochum et al. 2020). Pioneering experiments with species removals established a positive relationship between biodiversity and ecosystem function (Naeem et al. 1994, Hooper et al. 2005). However, those experiments did not entirely control for ‘sampling effects’, making it difficult to distinguish effects of species richness per se from



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effects of a few important species that would be more likely to be found in species-rich assemblages (O'Connor et al. 2017). Improved experimental designs manipulated species composition and species richness more systematically (Jochum et al. 2020), controlled for spatial scale and total abundance with substitutive designs (Thompson et al. 2018), and emphasized comparisons between monocultures and polycultures (Finney and Kaye 2017, Clark et al. 2019).

On the statistical side, analyses were also improved when Loreau and Hector (2001) modified the evolutionary Price equation (Price 1970, Frank 2012, Luque 2017) to provide a partitioning of ecosystem response variables into two additive components of complementarity (species richness) and dominance (species composition). Since Fox (2006) and Fox and Kerr (2012) first used Price partitioning to study specifically the effects of species loss and gain, the Price equation has become a standard tool in the study of animal and plant community functioning (Winfree et al. 2015, Genung et al. 2017, Bannar-Martin et al. 2018, Isbell et al. 2018, Koffel et al. 2020). van Veelen et al. (2012) and Pillai and Gouhier (2019) have recently criticized the Price partition for using a null expectation based on neutrality, and for failing to incorporate non-linearity, but major elements of this critique have not stood up to detailed scrutiny (Frank 2012, Luque 2017, Loreau and Hector 2019, Wagg et al. 2019). Additionally, Barry et al. (2019) have noted that complementarity (typically expressed as overperformance of diverse plots compared to monocultures) could reflect resource partitioning, abiotic facilitation or biotic feedbacks, making unequivocal interpretation challenging.

Perhaps a more substantive limitation is that the Loreau and Hector (2001) partition of the Price equation considers only changes in species richness and species composition, without incorporating effects of shifts in relative abundance and individual trait expression (Fox 2006, Fox and Kerr 2012, but see Genung et al. 2017). In earlier studies, this was not a serious constraint because traditional measurements of ecosystem function, such as above- and below-ground biomass, nutrient retention and microbial activity, were 'whole plot' measurements that could not be partitioned among individuals (Hector et al. 1999, Tilman et al. 2001). Moreover, many of the first experimental studies were made in temperate grassland systems with clonally growing grasses that cannot be distinguished as 'individuals' (Tilman et al. 2001). For these systems, the Loreau and Hector (2001) Price partition was useful because it matched the kind of data that were available.

But over the past 20 years, a new focus on trait-based approaches has highlighted that measures of ecosystem function ultimately reflect the traits and properties of individuals and species (Violle et al. 2007). Large data bases of species-level traits are now available for analysis, and there is growing interest in the simultaneous effects of within- and between-species variation in traits (Carlucci et al. 2015, Umaña and Swenson 2019).

In this paper, we build on the Loreau and Hector (2001) framework, and extend the Price equation partition to incorporate the relative abundance of each species. Our method uses data on individual traits, such as seed size or leaf area,

measured at either the individual or the species level. This derivation leads to five additive partitions that measure the single and combined effects of species richness, species composition, species relative abundance, trait expressions and total abundance. We illustrate the partition with a simulation study and a worked example using a large data set on early plant succession (Zaplata et al. 2013). We use the new Price partitioning to illustrate the behaviour of each partition in simulated assemblages, and how community trait values changes in time. Specifically, we address two important questions:

- 1) How is the change in total trait value partitioned into effects of species richness, composition and abundance?
- 2) Does the importance of each of these drivers predictably change in time during plant succession?

Methods

Abundance-based Price decomposition

Changes in the total trait value T between two communities can be additively decomposed into several partitions (Fox 2006). Our analyses consider a single trait, such as seed-size or body mass, that can be estimated on a continuous scale for individuals or species from two communities. Such a decomposition can be applied to spatial or temporal variation in assemblages. The total trait value T is assumed to be the sum of each single trait values at the individual or species level. Fox (2006) showed that the difference in total trait value ($\Delta T = T_B - T_A$) between two communities A and B that contain S_A and S_B species each out of a total of S_{total} species, and that have average trait expressions per species z_A in community A and z_B in community B is given by:

$$\begin{aligned} \Delta T &= S_B z_B - S_A z_A = S_B (\Delta z + z_A) - (-\Delta S + S_B) z_A \\ &= z_A \Delta S + S_B \Delta z \end{aligned} \quad (1)$$

where $\Delta z = z_B - z_A$. If the abundance of species i in a community is n_i , then the total abundance $N = \sum n_i$, and the relative abundance of species i is naturally defined as $p_i = n_i / N$. Similarly, we define the average trait expression for all of the individuals of species i in a community as c_i , the total (summed) trait value of the community $T = \sum t_i = \sum n_i c_i$. The average community trait expression z_A of community A comes from the weighted mean $z_A = \frac{T_A}{S_A} = \frac{N_A}{S_A} \frac{\sum n_{A,i} c_{A,i}}{N_A} = \frac{N_A}{S_A} \sum_i p_{A,i} c_{A,i}$. Algebraic reordering results in a decomposition of the difference in trait expression (full proof in Supporting information):

$$\begin{aligned} \Delta T &= z_A \Delta S + N_B \sum_i \Delta p_i \Delta c_i + N_B \sum_i p_{A,i} \Delta c_i \\ &\quad + N_B \sum_i \Delta p_i c_{A,i} + \left(N_B - N_A \frac{S_B}{S_A} \right) \sum_i p_{A,i} c_{A,i} \end{aligned} \quad (2)$$

With the common definition of the mathematical expectation calculated either over all species (E_S) or those present in community A (E_{S_A}), we obtain a simplified notation:

$$\Delta T = E_{S_A}(c_A)\Delta S + N_B E_S(\Delta p \Delta c) + N_B E_S(\Delta c) + N_B E_C(\Delta p) + f(\Delta N)E_S(t_A) \quad (3)$$

t_A refers to the species trait value in A. E_C indicates that the expectation of Δp is weighted by the trait expression. Below we refer to these partitions as $\prod(\Delta S)$, $\prod(\Delta p \Delta c)$, $\prod(\Delta c)$, $\prod(\Delta p)$ and $\prod(\Delta N)$, respectively. We note that the first term of our partitioning equals the species richness term and that the three middle terms are equivalent to the context-dependent effect in Fox (2006). The fifth term reflects a richness–abundance interaction that can be further decomposed (described later) to include only an abundance term.

Equation 2 incorporates relative species abundances and relative trait expressions and does not rely on species losses and gains, which is in contrast to existing ecological partitions of the Price equation (Fox 2006, Fox and Kerr 2012,

Genung et al. 2017, Bannar-Martin et al. 2018), Our method decomposes the difference in total trait expression between two communities (the respective total trait values) into five components:

- 1) the difference in species richness $\prod(\Delta S)$
- 2) the average difference in species trait expression $\prod(E_S(\Delta c))$
- 3) the trait-weighted difference in relative abundance $\prod(E_C(\Delta p))$
- 4) the combined effect of differences in relative trait abundance and changes in trait expression $\prod(E_S(\Delta p \Delta c))$
- 5) the effect of differences in abundance $\prod(\Delta N)$.

Importantly, this approach does not rely on a covariance decomposition (Fox 2006, Genung et al. 2017) between trait and species occurrence, which has been recently criticized (Pillai and Gouhier 2019). Of course, the term $E_S(\Delta p \Delta c)$ is identical to the covariance of Δp and Δc after adding the constant $E_S(\Delta p)E_S(\Delta c)$. The term $E_S(\Delta p \Delta c)$ accounts for the correlation between the differences in relative trait expression and relative abundance. It can be interpreted as community-wide differences in dominance structures due to species

Box 1. Summary of equations, constraints on input variables (traits, species richness and abundance), and short comments on application

Equation	Expression	Richness data	Abundance data	Trait data	Comments
2	$\Delta T = z_A \Delta S + N_B \sum_i \Delta p_i \Delta c_i + N_B \sum_i p_{A,i} \Delta c_i + N_B \sum_i \Delta p_i c_{A,i} + \left(N_B - N_A \frac{S_B}{S_A} \right) \sum_i p_{A,i} c_{A,i}$	$S_A, S_B > 0$	$N_A, N_B > 0$	$c_{iA}, c_{iB} \geq 0$	Unconstrained five partition solution. For $N_A \neq N_B$ the fifth partition quantifies the importance of ΔN
2+4	$\Delta T = z_A \frac{S_A}{N_A} \Delta N + N_B \sum_i \Delta p_i \Delta c_i + N_B \sum_i p_{A,i} \Delta c_i + N_B \sum_i \Delta p_i c_{A,i}$	$S_A, S_B > 0$	$N_A, N_B > 0$	$c_{iA}, c_{iB} \geq 0$	Unconstrained four partition solution with ΔN partition only
5	$\Delta T \approx N_B E_S(\Delta p \Delta c) + N_B E_S(\Delta c) + N_B E_C(\Delta p)$	$S_A, S_B > 0$	$N_A \approx N_B$	$c_{iA}, c_{iB} \geq 0$	Data with similar total abundances
6	$\Delta T = E_{S_A}(c_A)\Delta S + N_B E_C(\Delta p) + f(\Delta N)E_S(t_A)$	$S_A, S_B > 0$	$N_A, N_B > 0$	$c_{iA} = c_{iB}$	Data with invariant traits for all species
7	$\Delta T = N_A E_C(\Delta p)$	$S_A, S_B > 0$	$N_A \approx N_B$	$c_{iA} = c_{iB}$	Invariant traits for all species, similar total or relative abundance data
8	$\Delta T = E_{S_A}(c_A)\Delta S$	$S_A, S_B > 0$	$n_{iA}, n_{iB} \in \{0,1\}$	$c_{iA} = c_{iB}$	Invariant traits and presence–absence data
10	$\Delta T = \sum_i \Delta p_i^2 + 2 \sum_i p_{A,i} \Delta p_i = \sum_i (p_{B,i}^2 - p_{A,i}^2)$	$S_A, S_B > 0$	$N_A = N_B = 1$	$c_{iA} = p_{iA}$ $c_{iB} = p_{iB}$	Change in co-occurrence expressed as the difference in Simpson diversity
10	$\sum_i \Delta p_i^2 = \left(\frac{a}{S_A} + \frac{b}{S_B} \right)$	a, b : species only in A, B $S_A, S_B > 0$	$n_{iA}, n_{iB} \in \{0,1\}$	$c_{iA} = p_{iA}$ $c_{iB} = p_{iB}$	Change in co-occurrence of species presences–absences

interactions. Box 1 contains a summary of the approach together with important special cases discussed below.

Interpretation of the abundance term

Partition (5) reflects the difference in total abundances and therefore may reflect differences in the carrying capacity between the communities not covered by previous decompositions. This term of Eq. 3 covers the change in total abundance ΔN and has no direct equivalent in Fox (2006). In Fox's (2006) analysis, the third partition is interpreted as a pure compositional effect without direct reference to abundance although further decomposition of this partition includes an abundance term (Fox 2006). Note that the first and the last term of Eq. 2 can be combined using $z_A = \frac{N_A}{S_A} \sum_i p_{A,i} c_{A,i}$. Therefore:

$$\begin{aligned} z_A \Delta S + \left(N_B - N_A \frac{S_B}{S_A} \right) \sum_i p_{A,i} c_{A,i} &= z_A S_A \left(\frac{N_B}{N_A} - 1 \right) \\ &= z_A S_A \left(\frac{\Delta N + N_A}{N_A} - 1 \right) = z_A \frac{S_A}{N_A} \Delta N \end{aligned} \quad (4)$$

This algebraic reordering demonstrates that the richness and the abundance partitions are closely related, and we can obtain a single partition that covers the effects of differences in abundance. In other words, the fifth partition allows for a rescaling of the richness term into a true abundance term. For $N_B = N_A$, this combined term becomes zero (see below the treatment of this special case), otherwise it changes proportionally to the difference in abundance.

Although this algebraic reordering eliminates the richness term in Eq. 2, we are most often interested in the differences of both richness and abundance. The fifth term of Eq. 2 alone is a true abundance term in two cases: 1) where $S_B = S_A$ (simplifying the fifth term into $(\Delta N E_S(t_A))$); and 2) where $S_B \neq S_A$ and $N_B \neq N_A$. To see this, we note that the increase in species richness S with total abundance N , in accordance with a species accumulation curve (Colwell and Coddington 1994), can be approximated by a power function (Flather 1996). Therefore,

$$\frac{S_B}{S_A} = \left(\frac{N_B}{N_A} \right)^v, \text{ where } v \text{ is a constant. We substituted this}$$

relationship and $\Delta N = N_B - N_A$ into the last term of Eq. 2. Assuming that ΔN is small in comparison to N_A , the first two terms of a Taylor expansion of the binomial yield:

$$\begin{aligned} N_B - N_A \frac{S_B}{S_A} &= N_B - N_A \left(\frac{N_B}{N_A} \right)^v = N_A + \Delta N - N_A \left(1 + \frac{\Delta N}{N_A} \right)^v \\ &\approx N_A + \Delta N - N_A \left(1 + v \frac{\Delta N}{N_A} \right) = \Delta N (1 - v). \end{aligned}$$

The interpretation of the fifth term as the abundance term collapses when the difference in total abundance

between the two communities is zero ($N_B = N_A$) or relatively small ($N_A \approx N_B$) despite differences in species richness. In the case of relative abundance data, $N_B = N_A = 1$. Because

$$\sum_i p_{A,i} c_{A,i} = \frac{S_A}{N_A} z_A, \text{ the last term of Eq. 2 becomes}$$

$$\left(N_B - N_A \frac{S_B}{S_A} \right) \frac{S_A}{N_A} z_A = \left(\frac{N_B S_A}{N_A} - S_B \right) z_A \approx -(\Delta S) z_A. \text{ Therefore,}$$

the first and the last terms of Eq. 3 cancel out (exactly so if $N_B = N_A$, cf. example VII in Supporting information), and we obtain a three-partition solution that reflects the differences in species trait expression and relative abundances only:

$$\Delta T \approx N_B E_S (\Delta p \Delta c) + N_B E_S (\Delta c) + N_B E_C (\Delta p) \quad (5)$$

In this case the difference in trait value is predicted to be independent of the differences in richness and only reflects the differences in relative abundances and trait expression. Importantly, when using relative abundances N_A by definition equals N_B , leading directly to Eq. 5. This algebraic property offers a way to study differences in trait value directly without the need to account separately for differences in species richness. This property of the Price partitioning was not covered by previous approaches.

Special cases

As a first special case, we treat the situation when the trait expressions of each of the species do not differ between communities ($\Delta c_i = 0$ for all species i). This is often realised in ecological and biogeographic studies in which trait values are not measured directly from the samples, but are taken as species-level values from literature sources and trait data bases. In this case Eq. 3 simplifies to:

$$\Delta T = E_{S_A} (c_A) \Delta S + N_B E_C (\Delta p) + f(\Delta N) E_S (t_A) \quad (6)$$

Equation 6 predicts that the difference in total community trait value between two communities is an additive combination of the differences in richness, trait weighted average species relative abundance, and the richness–abundance interaction effect. If, additionally, total abundances are identical between the two focal communities ($N_B = N_A$), Eq. 6 in combination with Eq. 5 predicts that the difference in total trait value is solely defined by the difference in relative abundance and the initial values of richness and abundance because the first and last partition have an equal contribution to the change in community trait value.

$$\Delta T = N_A E_C (\Delta p) \quad (7)$$

Equation 7 does not reflect our intuition because it implies that the change in total community trait value is independent of changes in species richness if both communities have

identical total abundances. In fact, the richness effect goes into the Δp term. However, for presence–absence data, the terms $\left(N_B - N_A \frac{S_B}{S_A}\right)$ and $S_B E_C(\Delta p)$ of Eq. 6 become zero, and we obtain:

$$\Delta T = E_{S_A}(c_A)\Delta S \quad (8)$$

Therefore, in the case of constant species trait expressions and presence–absence data, the difference in total trait community value between communities A and B (ΔT) will only depend on the change in richness, in accordance with our intuition.

In the case of relative abundance data as trait values (rescaled abundance data $N_A = N_B = 1$), the five-component partition of Eq. 3 reduces to:

$$\Delta T = \frac{\sum_i p_{A,i}^2}{S_A} \Delta S + \sum_i \Delta p_i^2 + 2\sum_i p_{A,i} \Delta p_i + \left(1 - \frac{S_B}{S_A}\right) \sum_i p_{A,i}^2 \quad (9)$$

The first and the last partition cancel out (above) and Eq. 9 becomes:

$$\Delta T = \sum_i \Delta p_i^2 + 2\sum_i p_{A,i} \Delta p_i = \sum_i (p_{B,i}^2 - p_{A,i}^2) \quad (10)$$

This latter term comes from a binomial expansion. Because Simpson diversity is defined as the sum of squared relative species abundances, our partition implies that the change in the pattern of pairwise co-occurrences in abundance is expressed by the difference in Simpson diversity between communities B and A . Because our approach links Simpson diversity and species co-occurrences, it is related to work by Frank and Godsoe (2020) and Godsoe et al. (2021), who demonstrated that an extended Price equation can partition differences in Simpson and other Hill number diversity indices into differences in frequency and measurement.

Finally, this approach to co-occurrence (Eq. 10) can be applied to presence–absence data. In this case, ΔT equals the difference in species richness. Let a be the number of species that occur only in community A and b be the respective number in community B . The first term of Eq. 10 becomes

$$\sum_i \Delta p_i^2 = \left(\frac{a}{S_A} + \frac{b}{S_B}\right). \text{ The second term consequently reduces to } \sum_i p_{A,i} \Delta p_i = -\frac{a}{S_A} - \frac{b}{S_B}. \text{ In a fully segregated pattern, } a = S_A$$

and $b = S_B$, the first term of Eq. 10 has a maximum value of 2 (and a minimum of 0). In a fully nested pattern, where B is a true subset of A , the first term of Eq. 10 becomes $\frac{a}{S_A} < 2$.

Therefore, with presence–absence data, Eq. 10 partitions the gradient from nestedness to full segregation into two parts that contain the number of species exclusive to A and the number of species exclusive to B .

Simulation study

Supporting information contains seven simple worked examples for the calculations of the partitions. For a more detailed analysis of the behaviour of each partition, we additionally created six artificial community data sets (meta-communities) consisting of 10 single communities each. Each community had 5–50 species (species number assigned from an equiprobable random distribution). Species abundances in each of the six meta-community sets were created from crossing two species abundance distributions (SAD: log series and lognormal) and three co-occurrence structures (fully nested, equiprobable random and segregated). Species of each community were assigned trait values from an equiprobable random distribution, where trait values of single species within each meta-community were allowed to vary either by 20%, or by 50%, or by 100%, resulting in $3 \times 2 \times 3$ (occurrence structure \times abundance distribution \times trait values) meta-community trait variability combinations and a total of $k = 3 \times 2 \times 3 \times 10 \times 9/2 = 810$ pairwise combinations of communities to calculate ΔT and the respective partitions. We calculated for each combination the parameters of Eq. 3 using a Fortran application (source code available from WU by request). Additionally, we calculated for all these pairs the difference in Shannon diversity (ΔH) and the Bray–Curtis measure of structural similarity (BC). The Supporting information contains an R (ver. 4.0.3) function for calculating the partition.

Case study

From 2005 to 2011, we studied the early vegetation succession of a six ha area, the constructed catchment Chicken Creek (German: Hühnerwasser) within the partly decarburised lignite mine Welzow Süd in NE Germany (details in Gerwin et al. 2009). For this analysis, we used quantitative plant surveys from 426 non-contiguous single plots of 1 m² (Fig. 1, details in Zaplata et al. 2013) based on cover degree (abundance) according to a modified Londo scale (Londo 1976). Average plot species richness and average total abundances constantly increased during the seven years of succession (Zaplata et al. 2013). The complete data of species identities and abundances of all study years used in this study are already contained in Ulrich et al. (2014). Here, we partition the annual expression of specific leaf area (obtained from Leda; Kleyer et al. 2008). Because trait values for each species were obtained from the literature, our partition uses Eq. 5 only.

Statistical inference

Raw scores of ΔT and its partitions might depend on total species richness and abundances and also on the pattern of species overlap between the focal communities. Absolute values of the partitions might therefore be constraint by these boundary conditions and cannot be compared directly. Therefore, we need a statistical standard with which observed partition values can be compared. Many such null

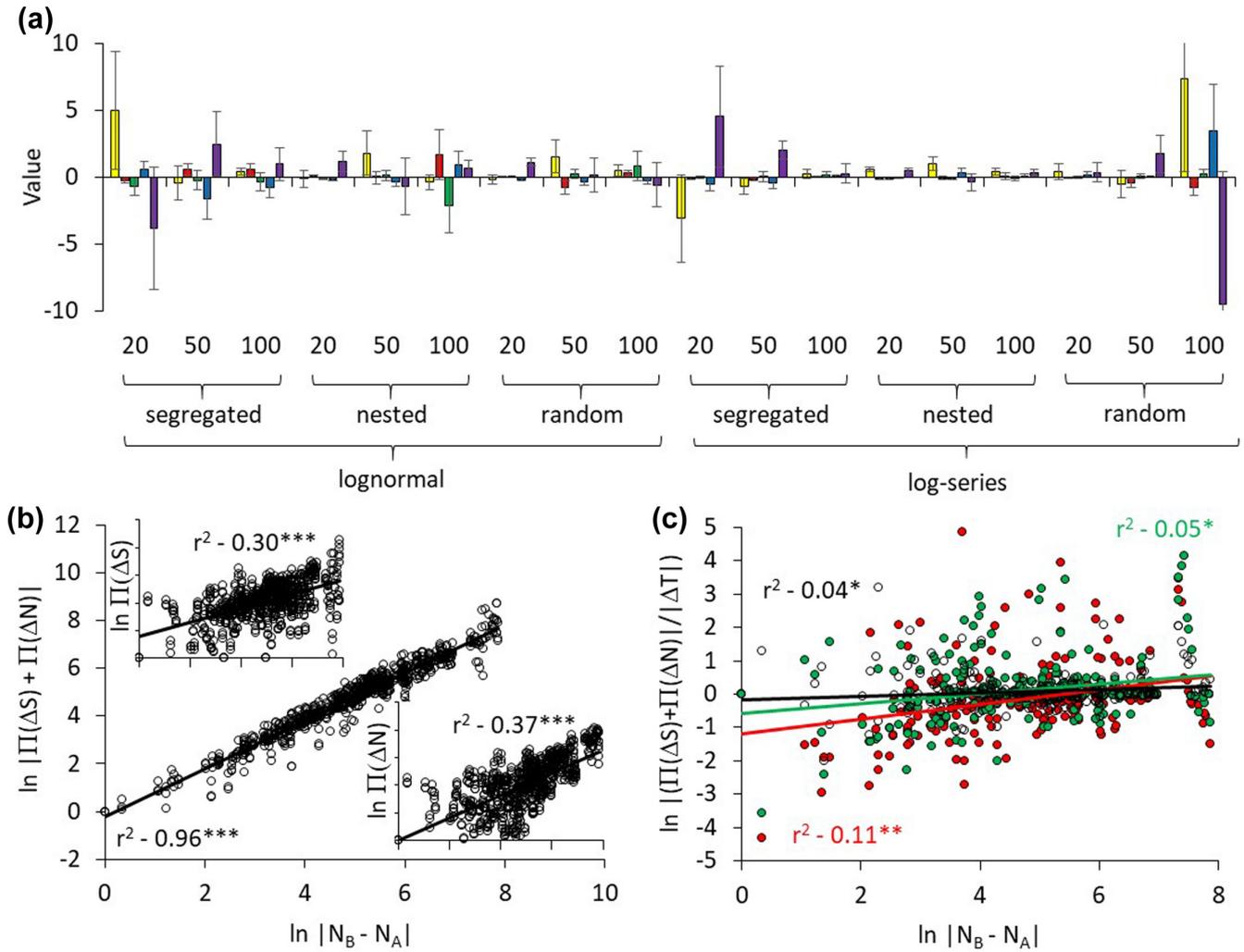


Figure 1. (a) Quotients of $\Pi(\Delta S)/\Delta T$ (yellow), $\Pi(\Delta c\Delta p)/\Delta T$ (red), $\Pi(\Delta c)/\Delta T$ (green), $\Pi(\Delta p)/\Delta T$ (blue) and $\Pi(\Delta N)/\Delta T$ (violet) with respect to abundance distribution (lognormal–log-series), pattern of co-occurrence (segregated–nested–random) and trait variability (20, 50, 100%) of 810 simulated communities. Error bars denote parametric standard errors. (b) Respective regressions of the sums of $\Pi(\Delta S)$ and $\Pi(\Delta N)$ with the $N_B - N_A$ (inlets show single regressions of $\Pi(\Delta S)$ and $\Pi(\Delta N)$, respectively. Regression main figure: $Y = 1.002X + 0.25$). (c) Proportion the absolute value based Price partitions $\Pi(\Delta S) + \Pi(\Delta N)$ to ΔT in dependence of the $N_B - N_A$. Open dots: low trait variability, green dots: intermediate variability, grey dots: high variability. Values in (b) and (c) are ln-transformed. Parametric significances: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

or neutral standards have been proposed so far, and those that constrain important boundary conditions like total abundances and species richness were found to be least biased (reviewed in Ulrich and Gotelli 2013, Ulrich et al. 2017, 2018). However, the present and prior Price decompositions contain richness and abundance in at least one of their terms, which would distort effect sizes obtained from null models that constrain these values (Ulrich et al. 2017). Randomizations of trait values only or reshuffling of species identities cannot serve as valid statistical standards for the present Price decomposition because these algorithms either fix community species richness or abundances, which causes the first and the last partition to always equal zero. Consequently, we need a baseline without constraints on species richness, and total abundances and numbers of

occurrences. Therefore, we applied a relaxed randomization algorithm that equiprobably reshuffled species occurrences among communities. We used standardized effect sizes $SES = \frac{x - \mu}{\sigma}$; where x is the partition value, and μ and σ refer to the respective arithmetic mean and standard deviation of the partitions of the random distribution. We note, that the arithmetic means of the null distribution for the $\Pi(\Delta S)$ and $\Pi(\Delta N)$ partitions asymptotically achieve $\Pi(\Delta S) = \Pi(\Delta N) = 0$.

We analysed the simulated data with general and generalized linear modelling. We used an identity link function and normal error structure in combination with AIC models election as implemented in STATISTICA 12 to relate the changes in trait value to variation among simulated assemblages in

Table 1. Dependence of the Price partitions on important community attributes of the simulated communities. General linear modelling showing parameter (β) values, partial η^2 values, the coefficient of determination of the whole model (r^2), and parametric significances. Error degrees of freedom $df=791$. BC: structural similarity quantified by the Bray–Curtis metric. ΔH : difference in Shannon diversity, SAD: type of species abundance distribution (log-series, lognormal), structure: type of community assembly (nested, segregated, random), trait variability: low, medium, high.

Variable	df	ΔT			$\prod(\Delta S)$			$\prod(\Delta c\Delta p)$		
		β -value	Partial η^2	P	β -value	Partial η^2	p	β -value	Partial η^2	p
BC	1	< 0.01	< 0.01	0.97	0.16	0.06	< 0.001	-0.02	< 0.01	0.64
ΔH	1	0.03	< 0.01	0.72	-0.10	< 0.01	0.12	-0.15	< 0.01	0.20
S_A	1	0.02	< 0.01	0.86	-0.03	< 0.01	0.62	0.09	< 0.01	0.45
N_A	1	-0.03	< 0.01	0.56	0.05	< 0.01	0.19	-0.01	< 0.01	0.95
T_A	1	-0.74	0.22	< 0.001	-0.86	0.41	< 0.001	-0.09	< 0.01	0.20
SAD	1		0.07	< 0.001		< 0.01	0.51		< 0.01	0.11
Structure	2		0.04	< 0.01		0.08	0.00		0.01	0.10
Trait variability	2		0.01	0.09		< 0.01	0.41		0.01	0.01
SAD \times Structure	2		0.04	< 0.01		0.02	< 0.01		0.01	0.05
SAD \times Trait	2		< 0.01	0.16		< 0.01	0.92		0.01	0.02
Structure \times Trait	4		0.02	0.01		< 0.01	0.80		0.03	< 0.01
r^2	791		0.52	< 0.001		0.73	< 0.001		0.07	< 0.001

Variable	df	$\prod(\Delta c)$			$\prod(\Delta p)$			$\prod(\Delta N)$		
		β -value	Partial η^2	P	β -value	Partial η^2	p	β -value	Partial η^2	p
BC	1	0.07	< 0.01	0.06	0.19	0.02	< 0.01	-0.21	0.04	< 0.01
ΔH	1	0.21	< 0.01	0.19	-0.15	< 0.01	0.18	0.20	0.01	0.04
S_A	1	-0.16	< 0.01	0.44	0.07	< 0.01	0.53	0.01	< 0.01	0.92
N_A	1	0.06	< 0.01	0.60	0.32	0.02	0.01	-0.25	0.02	< 0.01
T_A	1	-0.04	< 0.01	0.08	-0.41	0.05	< 0.01	-0.33	0.04	< 0.01
SAD	1		0.01	0.01		0.01	0.02		0.12	< 0.001
Structure	2		0.01	0.01		0.07	< 0.001		0.05	< 0.01
Trait variability	2		0.03	0.32		0.01	0.01		< 0.01	0.81
SAD \times Structure	2		0.01	0.01		0.04	< 0.01		0.03	< 0.01
SAD \times Trait	2		0.02	0.01		0.01	0.04		< 0.01	0.80
Structure \times Trait	4		0.02			0.01	0.08		< 0.01	1.00
r^2	791		0.09	< 0.001		0.17	< 0.001		0.34	< 0.001

species richness (S_A), total trait expression (T_A) and abundances (N_A), patterns of diversity and co-occurrence, and the categorical treatments variables (pattern of co-occurrence, abundance distribution and magnitude of trait variability).

Results

Simulations

In the simulations, absolute values of ΔT and the five partitions were largely independent of the patterns of co-occurrence among model communities, type of SAD, and the variability in species trait expression (Table 1). Total species richness and abundances did not significantly influence the partitions (Table 1). However, the simulated assemblages generated significant negative correlations between T_A and ΔT , $\prod(\Delta S)$, $\prod(\Delta p)$ and $\prod(\Delta N)$ although the effect size of these partitions on ΔT differed (Table 1). Thus, larger initial total trait values were linked to smaller changes in ΔT and its partitions.

The proportional influences of the five partitions varied considerably among the simulations (Fig. 1a). General linear modelling revealed, however, a significant influence of the underlying species abundance distributions and the pattern of

co-occurrence on the changes in total trait value (Supporting information). Again, trait value was a strong correlate for all of the partitions, except for the changes in species richness.

Table 2. Dependence of ΔT on important community attributes of the simulated communities. General linear modelling showing parameter (β) values, partial η^2 values, the coefficient of determination of the whole model (r^2), and parametric significances. Error degrees of freedom $df=791$.

Variable	df	β -value	Partial η^2	p
SES ΔS	1	0.42	0.52	< 0.001
SES $\Delta c\Delta p$	1	0.28	0.55	< 0.001
SES Δc	1	0.09	0.11	< 0.001
SES Δp	1	0.28	0.57	< 0.001
SES ΔN	1	0.76	0.88	< 0.001
S_A	1	-0.01	< 0.01	0.12
N_A	1	-0.19	0.13	< 0.001
T_A	1	0.30	0.22	< 0.001
SAD	1	-	< 0.01	0.72
Structure	2	-	< 0.01	0.95
Trait variability	2	-	< 0.01	0.78
SAD \times Structure	2	-	< 0.01	0.33
SAD \times Trait	2	-	< 0.01	0.42
Structure \times Trait	4	-	< 0.01	0.01
r^2	791	-	0.95	< 0.001

We found a highly significant negative linear relationship (OLS regression: $\Pi(\Delta S) = (-0.95 \pm 0.03) \Pi(\Delta N)$; $r = -0.96$) between $\Pi(\Delta S)$ and $\Pi(\Delta N)$ at $\Delta N < 20$ individuals between communities A and B . Even at 100 individuals, $\Pi(\Delta S)$ and $\Pi(\Delta N)$ were correlated by $r = -0.67$. Importantly, the simulations returned a strong linear relationship between the sum of the $\Pi(\Delta S)$ and $\Pi(\Delta N)$ partitions and the difference in absolute abundance $N_B - N_A$: $|\Pi(\Delta S) + \Pi(\Delta N)| = 0.8|N_B - N_A|$, (Fig. 1b). $\Pi(\Delta S)$ and $\Pi(\Delta N)$ alone were much weaker correlated with $|N_B - N_A|$ (Fig. 1b inlets), a relationship that is not obvious from Eq. 5.

Finally, the combined effect of the partitions based on absolute values ($\Pi(\Delta S) + \Pi(\Delta N)$), and therefore the difference in absolute abundance, was in the minority of cases (42.3%, Fig. 1c) more important than the combined effect of the three partitions based on relative values ($\Pi(\Delta c\Delta p)$, $\Pi(\Delta c)$, $\Pi(\Delta p)$). Irrespective of the degree of trait variation, the importance of $\Pi(\Delta S)$ and $\Pi(\Delta N)$ increased with increasing difference in abundances (Fig. 1c).

When comparing the partitions with the equiprobable randomization test, we found highly significant effects of all partitions on ΔT (Table 2). Again, the most important partition was the change in total abundance (Table 2). The SES scores also identified the strong influence of changes in relative abundances $\Pi(\Delta p)$. The randomization removed the influence of the abundance distribution, the pattern of co-occurrence and the variation in traits on the partitions, but retained the influence of N_A (Table 2).

Case study

The average annual change in total trait value of species-specific leaf area was positive during the first six years of succession (Fig. 2) implying also a constant increase in

total SLA value. Because species richness and total abundance were positively correlated the same annual trend came up when comparing the trait partitions to absolute abundances (Supporting information). These changes could be separated into three partitions according to Eq. 5 (Table 3). Although the general linear model yielded highly significant impacts of total trait value, richness, abundance and study year, the effect sizes (partial η^2) were small except for the positive correlation of abundance with ΔT , $\Pi(\Delta S)$ and $\Pi(\Delta N)$, and the negative correlation of abundance with $\Pi(\Delta p)$.

The partitions of ΔT into components of $\Pi(\Delta S)$, $\Pi(\Delta p)$ and $\Pi(\Delta N)$ predictably changed during succession and exhibited two distinct phases (Fig. 2). During the first three years of the study, changes were comparatively moderate, and the increase in ΔT was driven by the respective increase in $\Pi(\Delta S)$ (Fig. 2). Beginning in year four (2008), there was a sharp increase in ΔT (Fig. 2). This two-phase picture of early succession was also mirrored by the variability among plots within each study year (quantified by the standard deviations from the 426 plots). For ΔT and $\Pi(\Delta p)$, these errors were small during the first three years of succession, but increased from the fourth year on (Supporting information). With respect to $\Pi(\Delta S)$ and $\Pi(\Delta N)$, this increase started already in 2007 (Supporting information).

The average temporal increase in ΔT was mainly driven by the respective change in $\Pi(\Delta N)$ and $\Pi(\Delta S)$, whereas the effect of $\Pi(\Delta p)$ decreased through time (Fig. 2). Importantly, the years 2007 and 2009 deviated from the trend of increasing ΔT , and our approach identified the change in average abundance ΔN as the most important factor (Fig. 2). As predicted from the partitioning, $\Pi(\Delta S)$ and $\Pi(\Delta N)$ exhibited opposing effects on ΔT (Fig. 2).

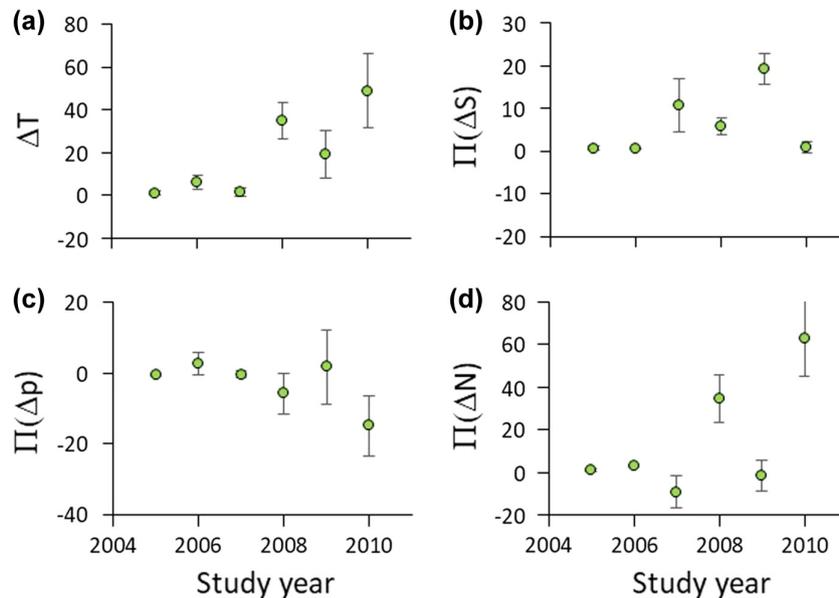


Figure 2. Annual trends in specific leaf area of ΔT , $\Pi(\Delta S)$, $\Pi(\Delta p)$ and $\Pi(\Delta N)$. Given are averaged values across all non-empty plots calculated for the series of adjacent pairs of years. Error bars denote parametric standard errors.

Table 3. General linear modelling indicates the highest influence of total abundances N_A on $\Pi(\Delta S)$, $\Pi(\Delta p)$ and $\Pi(\Delta N)$. Study year t and ΔT served as covariates. Given are β - and partial η^2 -values, the coefficient of determination of the whole model (r^2), and respective parametric significances. Error degrees of freedom $df=426$.

Variable	df	ΔT			$\Pi(\Delta S)$			$\Pi(\Delta p)$			$\Pi(\Delta N)$		
		β -value	Partial η^2	p	β -value	Partial η^2	p	β -value	Partial η^2	p	β -value	Partial η^2	p
T_A	1	-0.05	< 0.01	0.06	-0.17	< 0.01	< 0.001	-0.02	< 0.01	0.31	0.06	< 0.01	0.02
S_A	1	-0.05	< 0.01	0.01	0.04	< 0.01	0.01	0.08	< 0.01	< 0.001	-0.10	< 0.01	< 0.001
N_A	1	0.22	0.05	< 0.001	0.53	0.25	< 0.001	-0.30	0.11	< 0.001	0.27	0.07	> 0.001
Year	5	-	< 0.01	0.19	-	0.02	< 0.001	-	< 0.01	0.03	-	< 0.01	0.05
ΔT	1	-	-	-	-0.09	0.01	< 0.001	0.59	0.34	< 0.001	0.08	0.01	< 0.001
r^2	426	-	0.05	< 0.001	-	0.27	< 0.001	-	0.36	< 0.001	-	0.09	< 0.001

Discussion

In the BEF literature, complementarity and dominance reflect the way species partition limiting resources, but direct measurements of available resources are rare in such studies. However, resource partitioning itself should be reflected in the distribution of critical traits, both within and between species (McGill et al. 2006, Violle et al. 2007). We have shown that our new Price partition is able to decompose observed changes in total trait value into five straightforward and interpretable terms. Importantly, the new decomposition avoids problems related to the use of the covariance in prior decompositions (Pillai and Gouhier 2019). We have further shown that our approach covers absolute species abundances and does not rely on nested subsets of species as assumed in earlier approaches (Loreau and Hector 2001, Fox 2006, but see Fox and Kerr 2012). Our approach does also not require species overlap between the two communities (Fox 2006, Fox and Kerr 2012). These were important constraints on previous decompositions that made it difficult to use the Price partition for the comparison of differently-sized communities and of biogeographic data. In contrast, our partition can be used for any two communities, even for those without species overlap (cf. example VII in Supporting information). Finally, our approach covers changes in species trait expression in an intuitive and straightforward way. Earlier trait-based approaches (Fox and Harpole 2008) relied on a pre-partitioning multiple regression to define the average community trait expression. Genung et al. (2017) introduced a Price partitioning based on trait variation and abundance, similar to the present approach. However, their approach is based on a variance partition and the results cannot be easily interpreted in terms of richness, composition and abundance. Our approach combines relative trait expression, relative abundance data and absolute changes in species richness and total abundance in a general way that incorporates previous partitions as special cases.

As in some previous approaches, the $\Pi(\Delta S)$ term quantifies the contribution of the difference in species richness to ΔT . Because our partition uses abundance data, Eq. 3 contains a $\Pi(\Delta M)$ term that, in analogy to $\Pi(\Delta S)$, quantifies the contribution of the difference in absolute abundance. This term is particularly important in time series – here exemplified by primary succession – in which abundances constantly change. How these changes in abundance translate into changes of total trait value was not previously understood. Here we have shown that $\Pi(\Delta S)$ and $\Pi(\Delta M)$ are generally negatively correlated and even cancel out at small abundance differences between the two focal communities according to Eq. 5. Therefore, Eq. 5 predicts that with decreasing overall abundances, the relative impact of changes in richness on ΔT increases with respect to that of changes in abundance. Importantly, the $\Pi(\Delta S)$ partition is identical to the partition in Loreau et al. (2002) and Fox (2006). Those earlier methods were restricted to presence-absence data, in which the $\Pi(\Delta M)$ term equals zero and the $\Pi(\Delta S)$ term indeed covers the richness effect on traits. When dealing with abundances,

more complex interactions between richness and abundance have to be considered that are hidden behind the positive correlation between richness and abundance.

Any additive partitioning of a focal variable raises the question of cause and effect. The Price partitioning is a tautology in that sense that its derivation requires only the common definitions of the arithmetic mean and variance, and basic arithmetic operations. Nevertheless, it provides us with testable hypotheses about the process of temporal change in ecologically or evolutionary important variables (Gardner 2020). In our new partition, we have to ask whether richness differences cause differences in trait values or whether apparent or hidden processes trigger the distribution of trait values that we link to differences in richness and abundance after an appropriate partitioning. Can we identify the partitions on which these apparent or hidden variables act? Our simulation study indicates that we can indeed relate the partitions to underlying patterns of co-occurrence and abundance distributions that appeared to be the quantitatively most important determinants of total trait value (Table 1). Our GLM analysis indicated that the change in trait value mainly occurred via the richness path, whereas the pattern of co-occurrences influenced ΔT through its effect on relative abundance (Table 1). The dominance structure, quantified by the type of relative abundance distribution, influenced T_A mostly by the total abundance path (Table 1). In general, the change in species richness appeared to be the most important determinant of the changes in total trait values.

A surprising result from the simulation analyses is that the covariance of relative species abundance and relative trait expression ($\prod(\Delta p \Delta c)$) and the change in relative trait expression ($\prod(\Delta c)$) explained only a small and statistically insignificant part of the variance in ΔT (Table 1). Because our model communities covered a wide range of observed community structures, we argue that both terms might indeed be of minor importance in comparison to the three other partitions. The $\prod(\Delta p \Delta c)$ partition is comparable, although not equivalent, to the 'species composition effect' of Fox (2006) in analogy to the selection effect of the original Price formulation (Price 1995). Loreau and Hector (2001) interpreted this covariance in terms of competition, whereas Fox (2006) attributed the effect to non-random species loss.

The present approach allows for a more precise interpretation in terms of measurable differences in trait expression of single species and respective differences in the relative abundances. In the case that Δc and Δp are uncorrelated, the $\prod(\Delta c \Delta p)$ partition becomes nearly zero. A positive correlation of Δc and Δp implies that species with a large positive difference in abundance also increase the trait expression in line with the selection or competition interpretation of this partition (Loreau and Hector 2001). A negative correlation between Δc and Δp implies that traits of species that increase in relative abundance reduce the respective trait expression, which could be interpreted as competitive elimination of species with certain trait values.

$\prod(\Delta p)$ does not simply quantify the changes in relative abundances. In Eq. 2, $\prod(\Delta p)$ quantifies the change in

the relative contribution of a trait to the total trait value. Dominance of a single species with high trait value in community A will increase the total trait value. An increased evenness in B will tend to reduce the impact of the dominant species making the average to decrease and $\prod(\Delta p)$ to become negative. This is exactly what we have found in the case study (Table 3) and is consistent with a previous result that the species abundance distributions tend to become more even during early plant succession (Ulrich et al. 2014). Similarly, Cornwell et al. (2006) reported significant relationships between plant trait expression and relative abundance, including a negative correlation between abundance and SLA. Consequently, there was a tradeoff in total SLA expression between abundant and rare species resulting in comparatively small ΔT between these two abundance groups.

The Price partitioning is inherently affected by statistical averaging. For example, if species richness positively correlates with community evenness (Soininen 2014, Lembrechts et al. 2018), the total trait value becomes less influenced by the dominant species. Consequently, average trait values become increasingly independent of relative species abundances. This is what we found in our simulation study. Community species richness and evenness were significantly positively correlated ($r=0.39$, $p < 0.001$) and z_A and $\prod(\Delta p)$ were significantly negatively correlated below 30 species ($r=-0.22$, $p < 0.001$), while becoming independent at higher richness ($r=-0.02$, $p > 0.05$; not shown). Transferring this result to plant succession, we predict relative trait abundances to be of comparably minor importance for the difference in total trait value at later stages of plant succession.

$\prod(\Delta N)$ of Eq. 2 contains the value $\sum_i p_{A,i} c_{A,i}$. This term is identical to the definition of community-weighted mean functional traits CWM (Wright et al. 2004, Cornwell and Ackerly 2009). This concept has recently gained renewed interest (Miller et al. 2019) because it quantifies average local trait expression, which can be assumed to define a local fitness optimum (Shipley et al. 2011). Previous approaches to local species trait distributions compared CWM directly to species abundances (Muscarella and Uriarte 2016) or used correlations of CWM with environmental variables (Peres-Neto et al. 2017), although Miller et al. (2019) noticed that there are currently no overall best methods for the evaluation of trait environment relationships. Our approach opens the way to a dynamical assessment of CWM based on direct comparisons with changes in trait expression ($\prod(\Delta c)$) and effects of community composition ($\prod(\Delta p \Delta c)$) while inherently accounting for species richness and absolute abundances.

For the first time, we applied the Price partitioning to plant successional data to better understand which elements of temporal community change are most important at various states of succession. A major result of this analysis is the trade-off between the ΔS , Δp and ΔN , which causes each partition to be of major importance for the change in plant SLA at a different stage of succession (Fig. 2). We also found a marked transition in ΔT from the third to the fourth year of succession (Fig. 2) triggered by respective changes in total

abundance (Zaplata et al. 2013). That study also identified two major phases in early succession characterized by the alteration of dominant plant species. Here we extend on these results and show that these shifts are causing major changes in trait values and that such major phases in early plant succession can be identified by tracing the relative importance of different drivers of changes in total trait value.

Prior work on this system revealed a joint increase in total SLA and abundance during succession (Ulrich et al. 2014) and hinted to a similar positive correlation between abundance and average trait expression z_A . However, we could not confirm a simple richness effect on ΔT during succession after accounting for the effect of abundance N_A (Table 2). Earlier findings of an effect of species richness on ecosystem function based on presence–absence data may have been caused by underlying correlations with abundance. The expanded version of the Price partition that we have developed here should help ecologists to better understand the effects of species richness, composition and abundance on traits and ecosystem function.

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Author contributions

Werner Ulrich: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (lead); Software (lead); Supervision (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Markus K. Zaplata:** Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal). **Nicholas J. Gotelli:** Validation (equal); Writing – review and editing (equal).

Data availability statement

There are no new data in this publication. Raw data of the case study are fully contained in Ulrich et al. (2014).

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