

ARTICLE

Quantifying interspecific and intraspecific diversity effects on ecosystem functioning

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Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 511084840

Handling Editor: Kerri M. Crawford

Abstract

Rapid environmental changes result in massive biodiversity loss, with detrimental consequences for the functioning of ecosystems. Recent studies suggest that intraspecific diversity can contribute to ecosystem functioning to an extent comparable to contributions of interspecific diversity. Knowledge on the relative importance of these two sources of biodiversity is essential for predicting ecosystem consequences of biodiversity loss and will aid in the prioritization of conservation targets and implementation of management measures. However, our quantitative insights into how interspecific and intraspecific biodiversity loss affects ecosystem functioning and how the effects of these two sources of biodiversity loss on ecosystem functioning can be compared are still very limited. To facilitate such quantitative insights, we extend the interspecific Price partitioning method originally introduced by J. Fox in 2006, previously used to quantify species loss and gain effects on ecosystem functioning, to also account for the effects of intraspecific diversity loss and gain on ecosystem function. Using this extended version can yield the quantitative information required for answering research questions addressing correlations between interspecific and intraspecific diversity effects on ecosystem functioning, identifying interspecific and intraspecific groups with large effects, and assessing whether intraspecific diversity can compensate for losses in interspecific diversity. Applying this method to carefully designed experiments will provide additional insights into how biodiversity loss at different ecological levels contributes to and changes ecosystem functioning.

KEYWORDS

ecosystem functioning, interspecific diversity, intraspecific diversity, Price equation

INTRODUCTION

Rapid environmental changes often result in massive biodiversity loss; currently, one million species are at risk of extinction (Díaz et al., 2019). Individual species and the

composition of communities provide important contributions to ecosystem functioning and human health (Cardinale et al., 2012; Díaz et al., 2018, 2019; Duffy et al., 2017; Naeem et al., 2009). Hence, the loss of biodiversity can dramatically reduce ecosystem health and nature's

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contributions to people's well-being (Brauman et al., 2020; Cardinale et al., 2012; Hooper et al., 2005; le Provost et al., 2023). In recognition of this problem, a central goal of biological conservation and management strategies is to anticipate and mitigate the impacts of environmental changes on biodiversity (Carvalho et al., 2019; Jones et al., 2016). Although biodiversity varies at multiple scales, the vast majority of such efforts have focused on the diversity of species per se (Des Roches et al., 2021; Laikre et al., 2020), as well as phylogenetic diversity among species.

Existing efforts thus tend to ignore the likely importance of diversity within species, that is, intraspecific diversity. First, just like species and phylogenetic diversity, intraspecific diversity can decrease under rapid environmental change—as documented by studies of genetic diversity (Exposito-Alonso et al., 2022; Leigh et al., 2019; Millette et al., 2020), population diversity (Ceballos et al., 2020), and phenotypic diversity (Raffard et al., 2021; Thompson et al., 2019). Second, intraspecific diversity is known to shape community structure and ecosystem function (Raffard et al., 2021)—and is sure to similarly influence nature's contributions to people (Des Roches et al., 2018; Raffard et al., 2019). For instance, various experimental studies across diverse taxonomic groups have shown that different ecotypes, populations, and genotypes can strongly alter population growth rates, community diversity (e.g., species richness, species diversity), and ecosystem functioning (e.g., primary productivity, nutrient cycling, decomposition, water clarity) (Bassar et al., 2010; Matthews et al., 2016; Pantel et al., 2015). Further, a meta-analysis of 25 studies that manipulated both interspecific and intraspecific diversity reported that ecological effects were often similarly strong at these two levels of diversity (Des Roches et al., 2018). In short, we still often ignore intraspecific diversity when considering the effects of environmental change on biodiversity and the resulting consequences for ecosystems and people (Des Roches et al., 2018, 2021; Laikre et al., 2020).

Importantly, interspecific and intraspecific diversity are not independent. First, the two levels of diversity are often (but not always; Puşcaş et al., 2008) positively correlated in natural communities (He et al., 2008; Vellend et al., 2014). Second, the effects of one level of diversity on ecosystem functioning may depend on the other level of diversity. For example, Crawford and Rudgers (2012) found that the relationship between interspecific diversity and the biomass of a whole plant community depended on the level of intraspecific diversity in the dominant plant species. Given these associations, it is critical to develop theory and tools that allow researchers to estimate the separate and combined effects of interspecific and intraspecific diversity on ecosystem functioning. Our goal in this paper is to contribute to these developments.

When ecosystem functioning comprises the summed functional contributions of the individuals within the

community, its value can change due to an increase or decrease in interspecific and/or intraspecific diversity. Such an increase or decrease can be caused by abundance changes (including gains or losses) of the interspecific groups (i.e., species) or the intraspecific groups (i.e., phenotypic groups within species) and changes in the functional contributions of particular interspecific and intraspecific groups. To build a framework for partitioning such effects, we can start with an existing interspecific Price equation approach (Fox, 2006; Fox & Kerr, 2012). Specifically, Fox (2006) and Fox and Kerr (2012) showed how changes in interspecific diversity contributed to changes in the ecosystem functioning of a community between two time points or between two communities at two distinct spatial locations. Here we extend this method to also consider changes in intraspecific diversity and, thus, allow for simultaneous assessment on the two levels of diversity in their effects on ecosystems.

Specifically, our method allows for a quantification of loss and gain effects when interspecific and intraspecific diversity is randomly lost or gained, of compositional effects due to nonrandom losses and gains of interspecific and intraspecific groups, and of context-dependence effects (CDEs) when the functional contribution of intraspecific groups differs between the communities of interest. We then showcase the applicability of the method using a previously published study by Weider et al. (2008) and by highlighting hypothetical data examples, which provide additional insights into the distinct components of this extended version. Last, we provide guidelines on the data collection for this method and highlight how the application of this method can yield quantitative information on research questions addressing the effects of interspecific and intraspecific diversity on ecosystem functioning. Specifically, by applying this method to multiple study systems, we will be able to determine whether there exist correlations between the effects of interspecific and intraspecific diversity and whether the distributions of effects for interspecific and intraspecific diversity are similar, in order to identify interspecific or intraspecific groups with large effects (e.g., identify “keystone genotypes” or “keystone genes,” which are genotypes or genes with disproportionately large ecological effects compared to their abundance; Barbour et al., 2022; Skovmand et al., 2018). Finally, we will be able to assess whether intraspecific diversity can compensate for losses in interspecific diversity and whether interspecific groups with large effects house intraspecific groups with large effects. We address each of these questions in detail. However, we start by briefly revisiting the interspecific Price equation introduced by Fox (2006) and show how it can be extended to include the effects of

intraspecific diversity. For illustrative purposes, we focus on the metric by Fox (2006), which only includes the effects of interspecific loss, but detail the extension to a second version of the interspecific Price equation by Fox and Kerr (2012) in Appendix S1: Section S1.

INTERSPECIFIC PRICE EQUATION (FOX, 2006)

The Price equation was developed to quantify evolutionary changes within a population, attributing the total population change to components of selection and transmission bias (Price, 1970, 1972). As pointed out by G. R. Price himself and others, the Price equation is a versatile tool; it can be used on any population characteristic of interest (Frank, 2018) but can also be easily extended to other situations. Indeed, different versions of the Price equation have been used in evolutionary biology (Queller, 2017), epidemiology (Day & Gandon, 2006), eco-evolutionary dynamics (Collins & Gardner, 2009; Ellner et al., 2011; Govaert et al., 2016), and community and ecosystem ecology (Fox, 2006, 2010; Fox & Kerr, 2012; Harrison et al., 2022). Fox (2006) used a Price equation approach to quantify the effects of changes in interspecific diversity on ecosystem functioning by separating the change in ecosystem functioning between two communities at two distinct time points or two distinct locations in space (referred to as the baseline and comparison community) into three components: species richness, species composition, and CDE. In this study, we proceed from this version of the Price equation. In addition, we will refer to these components as the interspecific richness, the interspecific composition, and the interspecific context-dependence effects. The interspecific richness effect (SRE) captures the effect by which the total ecosystem function would change when there is a random loss of interspecific groups at the baseline site (hence, a change in interspecific richness). The interspecific composition effect (SCE) quantifies the change in ecosystem function due to nonrandom loss of interspecific groups from the baseline site and indicates whether the interspecific groups that were lost contributed above or below average to ecosystem functioning. The CDE reflects the between-site difference in the functional contributions of interspecific groups common to both sites. For a more detailed explanation of each term, we refer the reader to Fox (2006).

An important assumption of this method is that the set of interspecific groups of the community at the comparison site is a subset of the interspecific groups at the baseline community, that is, $\{1, \dots, s'\} \subseteq \{1, \dots, s\}$, with s' representing the total number of interspecific groups at

the comparison community and s the total number of interspecific groups at the baseline community. Hence, in this version of the interspecific Price equation, we can only quantify effects due to loss of interspecific groups and not due to gain of interspecific groups, but see Fox and Kerr (2012) for an extension that does not require this assumption (also detailed in Appendix S1: Sections S1 and S2).

To obtain the metric of Fox (2006), assume a baseline and comparison community (either one community being measured at two distinct time points or two communities at two distinct spatial locations) with s (indexed by $i \in \{1, \dots, s\}$) and s' interspecific groups (indexed by $\{1, \dots, s'\} \subseteq \{1, \dots, s\}$), respectively. Second, assume that the ecosystem function of interest comprises the summed functional contributions of the individual interspecific groups. That is, if z_i is the functional contribution of interspecific group i in the baseline community, then the total value of the ecosystem function in the baseline community is given by the sum of the functional contributions of its interspecific groups, that is, $T = \sum_{i=1}^s z_i$. Similarly, if z'_i is the functional contribution of interspecific group i in the comparison community, then the total value of the ecosystem function at the comparison community is given by $T' = \sum_{i=1}^{s'} z'_i$. Furthermore, the average functional contribution per species of the baseline community can be calculated as $\bar{z} = \sum_{i=1}^s \frac{1}{s} z_i$. Hence, the total ecosystem function at the baseline community can also be written $T = s\bar{z}$. To calculate the mean functional contribution per interspecific group in the comparison community, we need a mathematical notation to retain the information about which interspecific group is lost. For this, we assign a weight w_i to z'_i , where $w_i = 0$ when the i th interspecific group is lost in the comparison community and $w_i = 1$ when the i th interspecific group is present in both communities. Thus, we calculate the average functional contribution per species in the comparison community as $\bar{z}' = (1/s') \sum_i w_i z'_i$, and the total ecosystem function at the comparison community as $T' = \sum_{i=1}^{s'} z'_i = s'\bar{z}'$. Following Fox (2006), the change or difference in total ecosystem function is then given by $\Delta T = T' - T$ and can be partitioned into three components:

$$\Delta T = \bar{z}\Delta s + \sum_{i=1}^s (w_i - \bar{w})(z_i - \bar{z}) + \sum_{i=1}^s w_i \Delta z_i, \quad (1)$$

with $\bar{w} = \frac{1}{s} \sum_{i=1}^s w_i$ and $\Delta z_i = z'_i - z_i$ the difference in the functional contribution of interspecific group i between the comparison and baseline communities. The first term on the right-hand side of Equation (1) represents the SRE. Here, $\Delta s = s' - s$, and $\bar{z}\Delta s$ thus reflects the change in ecosystem functioning due to a random loss of

interspecific groups as it multiplies the average functional contribution of all interspecific groups by the loss in the number of interspecific groups. This term reflects the functional effect of interspecific diversity loss that cannot be uniquely ascribed to a particular interspecific group (Fox & Kerr, 2012). The middle term on the right-hand side of Equation (1) represents the SCE and reflects the change in ecosystem function that is attributable to the nonrandom loss of interspecific groups. Specifically, it reflects the change in ecosystem function due to differences in interspecific composition between the baseline and comparison communities as opposed to changes in interspecific richness. Since it is calculated as a weighted difference between the functional contributions of the interspecific groups and the average contribution across interspecific groups, a negative value indicates that the interspecific group lost contributed on average more to the total ecosystem functioning, whereas a positive value indicates that the interspecific group lost contributed on average less to the total ecosystem function (see Fox & Kerr, 2012). The last term on the right-hand side of the equation represents the interspecific CDE and reflects the change in ecosystem functioning due to a difference in the functional contribution within the remaining interspecific groups between the two communities. This component encompasses effects due to intraspecific diversity, among others (see Fox [2006], but also detailed in the next section), which can be due to phenotypic plasticity or to a different composition of the intraspecific groups within the shared species. It is this third component that we will further extend to include effects of intraspecific diversity on ecosystem functioning (schematically presented in blue in Figure 1).

INTRASPECIFIC PRICE EQUATION

To extend the interspecific Price equation of Fox (2006) to include the effects of intraspecific diversity, we assume that for each of the interspecific groups we can identify distinct intraspecific groups. These groups can reflect distinct genotypes or clonal lineages when species of the interspecific groups reproduce asexually, genotypic groups of individuals defined by the presence or absence of specific genes or alleles, and phenotypic groups linked to distinguishable characteristics when species of the interspecific groups reproduce sexually. For example, intraspecific groups could comprise individuals of clonal lines of parthenogenetically reproducing *Daphnia* water flea species or individuals of the cress *Arabidopsis thaliana* varying in the metabolite aliphatic glucosinolate mainly determined by loss-of-function mutations at three specific genes (MAM1, AOP2, and GSOH; Barbour et al., 2022).

Depending on whether the ecosystem functional contributions are assessed in the field, via transplant experiments, or in the lab under controlled environments (e.g., via common garden experiments; Kawecki & Ebert, 2004), and depending on which intraspecific groups are considered (e.g., phenotypes vs. genotypes), the effects found can be attributed to intraspecific diversity in a broad sense (i.e., confounding genetic and plasticity effects) or to genetic diversity when distinct genotypes are used and functional contributions are quantified in such a way that they reflect genetic contributions only.

Similarly to Fox (2006), we consider baseline and comparison communities. For these communities, we assume that each i th interspecific group has a total of $G_i = \{1, \dots, G_i\}$ intraspecific groups, with the set of intraspecific groups within the i th interspecific group in the comparison community (G'_i) being a subset of G_i (but see Appendix S1: Sections S1 and S2 for an extension in which this assumption is not required). Analogously to how total ecosystem function of the community comprises the summed functional contributions of the interspecific groups, the total functional contribution of the i th interspecific group comprises the summed functional contribution of its intraspecific groups. Thus, for the baseline community, the total functional contribution of the i th interspecific group equals $z_i = \sum_j z_{ij}$, where z_{ij} is the functional contribution of intraspecific group j of interspecific group i . The average functional contribution of each i th interspecific group is then calculated as $\bar{z}_i = \frac{1}{G_i} \sum_{j=1}^{G_i} z_{ij}$. For the comparison community, we again need to consider those intraspecific groups that are lost. Hence, we use a weighting factor $w_{ij} = 1$ when the j th intraspecific group of interspecific group i is present in both the baseline and comparison communities and $w_{ij} = 0$ when the j th intraspecific group of interspecific group i is present in the baseline but absent in the comparison community. The average functional contribution of the i th interspecific group in the comparison community is then calculated as $\bar{z}'_i = \frac{1}{G'_i} \sum_{j=1}^{G'_i} w_{ij} z'_{ij}$. Applying the same calculations as in Fox (2006), we can partition the change or difference in the total ecosystem function for each interspecific group i into an intraspecific richness effect (IRE), an intraspecific composition effect (ICE), and an intraspecific context-dependence effect (ICDE), that is,

$$\Delta z_i = \bar{z}_i \Delta G_i + \sum_{j=1}^{G_i} (w_{ij} - \bar{w}_i) (z_{ij} - \bar{z}_i) + \sum_{j=1}^{G_i} w_{ij} \Delta z_{ij}. \quad (2)$$

In the first term on the right-hand side of Equation (2), $\Delta G_i = G'_i - G_i$. This first term reflects the change in ecosystem functioning within the i th interspecific group as a result of losing an intraspecific group at random and,

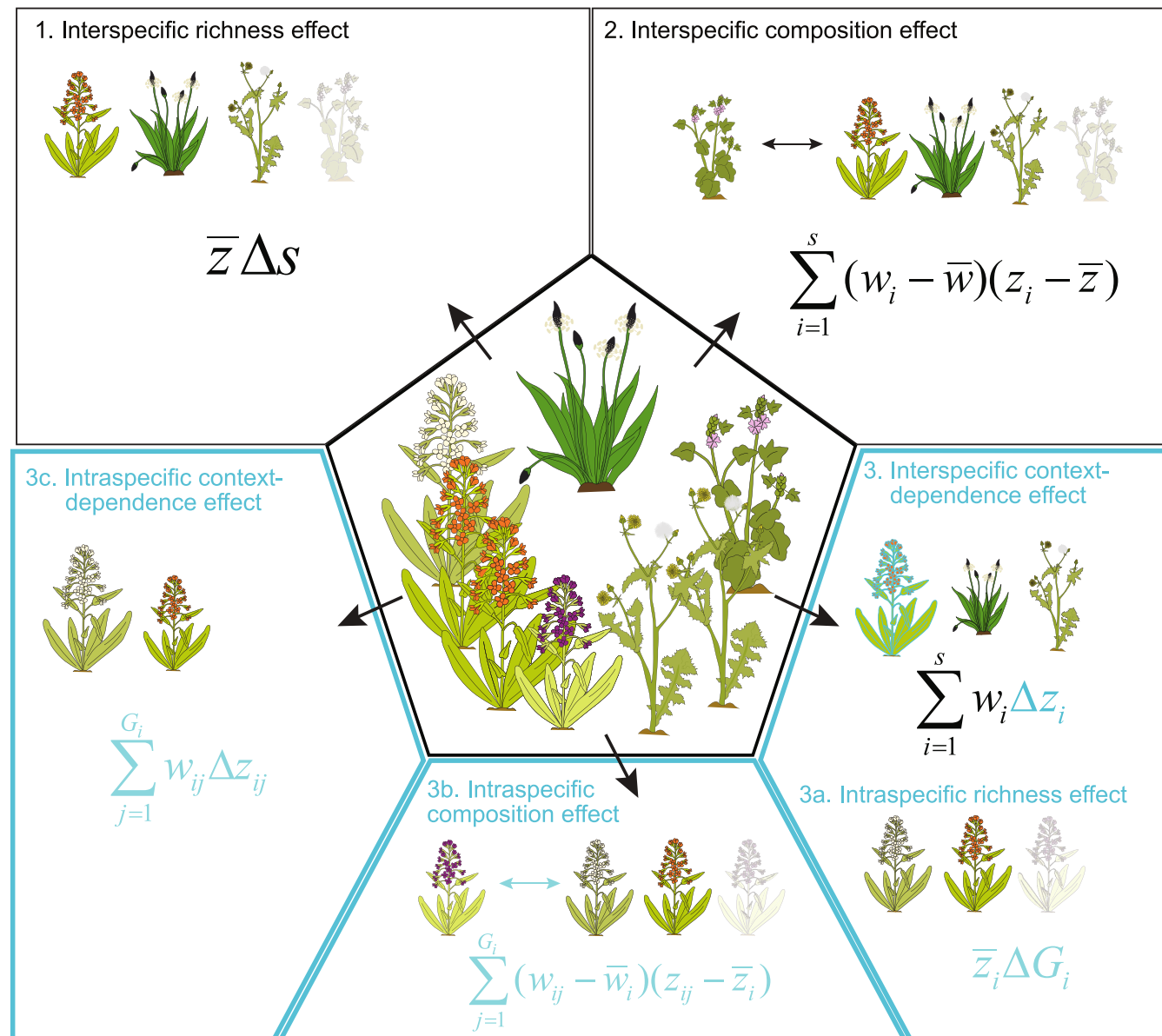


FIGURE 1 Conceptual visualization of Equation (4). Center pentagon represents a plant community consisting of four individuals of *Brassica* species, one individual of *Plantago* species, one individual of *Malva* species, and two individuals of *Sonchus* species. To demonstrate the effects of intraspecific diversity, for simplicity we assume that only the *Brassica* species has three distinct intraspecific groups. Each of the surrounding panels displays one of the terms in Equation (4). Arrows from the center to each outer panel reflect how the contribution of each term in Equation (4) is reflected by a change in the comparison community. The first panel represents the interspecific richness effect reflecting a change in ecosystem function due to a random loss of one or multiple interspecific groups (e.g., due to a random loss of *Malva* species) whose effect cannot be ascribed to a particular interspecific group. The second panel represents the interspecific composition effect, reflecting a change in ecosystem function due to nonrandom loss of interspecific groups. It reflects the group-specific effect on ecosystem function (e.g., how the lost *Malva* species contributed to ecosystem functioning compared to the other species, visually represented by the double arrow). The third panel represents the interspecific context-dependence effect and indicates within-interspecific group differences between the communities (e.g., whether interspecific groups increase or decrease in their functional contribution, here visually represented by different symbol sizes of the plant species). It is this term that we extended to include the effects of intraspecific diversity (in blue). For shared interspecific groups between the baseline and comparison community, the interspecific context-dependence effect can be decomposed into three components: (3a) the intraspecific richness effect, which reflects the change in ecosystem function due to random intraspecific diversity loss (e.g., if we lose the purple genotype of the *Brassica* species at random); (3b) the intraspecific composition effect, which reflects the change in ecosystem function due to specific loss of certain intraspecific groups (e.g., how the functional contribution of the purple genotype compares to the contribution of the other genotypes); and (3c) the ICDE, which reflects changes in the functional contribution within the remaining intraspecific groups (e.g., functional contributions of the white and orange genotype change, visualized by symbol size). Plant illustrations by Lynn Govaert.

hence, cannot be uniquely ascribed to a specific intraspecific group. It reflects how loss of intraspecific richness per se will alter the total ecosystem function contribution of the i th interspecific group, and we refer to this term as the IRE. The second term on the right-hand side of Equation (2) reflects a change in ecosystem function of the i th interspecific group due to nonrandom loss of its intraspecific groups. It reflects a change in the composition of intraspecific groups within the i th interspecific group between the baseline and comparison community. We refer to this term as the ICE. The last term on the right-hand side of Equation (2) relates to the ICDE and reflects the between-community difference attributed to a change in the functional contribution of particular intraspecific groups.

As mentioned in Fox (2006) for the interspecific CDE, here, too, the intraspecific context-dependence component reflects many different underlying mechanisms. First, the abundance of intraspecific groups may increase or decrease between the baseline and comparison community, resulting in an increase or decrease in the functional contribution of each corresponding intraspecific group (and, ultimately, of the interspecific group). Second, the per-capita functional contribution of each intraspecific group (i.e., the total functional contribution of each intraspecific group divided by its abundance) may differ between the community at the baseline and comparison sites. There are several reasons why intraspecific groups could differ in their per-capita functional contribution between the baseline and comparison community. Individuals within these intraspecific groups may express a different phenotype and, thus, functional contribution, depending on the environment they experience, also known as phenotypic plasticity (DeWitt, 1998). Phenotypic plasticity may occur as a consequence of a change in the abiotic as well as biotic environment. The latter includes the presence or absence of specific species (e.g., presence or absence of a predator species; Miner et al., 2005), but also changes in species composition could induce such a response, or even the presence or absence of other intraspecific groups and the individual composition of the intraspecific group itself (Lankau & Strauss, 2008; Pocco et al., 2019; Tollrian & Harvell, 1999). One example is *Brassica rapa*, which produces toxic allelopathic compounds to outcompete competitor species (Lankau & Strauss, 2008). However, the quantity of toxin produced depends on the amount of interspecific versus intraspecific competition *Brassica* experiences, that is, when intraspecific competition is high, toxin production is reduced. The per-capita functional contribution of an intraspecific group can also change due to pleiotropic effects, in which two or more traits share an underlying genetic basis and changes in a specific trait

lead to changes in the functional trait of interest. Lastly, mutations may also change the per-capita functional value of a particular intraspecific group. While in principle a mutation would result in a new genotype, practically this is not always detectable (Govaert et al., 2016). To gain some understanding of the processes that underlie the CDE, we can further partition the CDE quantified for interspecific group j following Fox (2006):

$$\sum_{j=1}^{G_i} w_{ij} \Delta z_{ij} = \sum_{j=1}^{G_i} \left(w_{ij} p_{ij} \Delta n_{ij} + w_{ij} n_{ij} \Delta p_{ij} + w_{ij} \Delta n_{ij} \Delta p_{ij} \right), \quad (3)$$

where $\Delta n_{ij} = n'_{ij} - n_{ij}$ reflects the difference in the abundance of intraspecific group j from the baseline (n_{ij}) to the comparison (n'_{ij}) community, $\Delta p_{ij} = p'_{ij} - p_{ij}$ reflects the difference in the per-capita functional contribution of intraspecific group j between the baseline (p_{ij}) and comparison (p'_{ij}) community, and $\Delta n_{ij} \Delta p_{ij}$ is the interaction between change in abundance and change in per-capita functional contribution of intraspecific group j .

COMBINING THE INTERSPECIFIC AND INTRASPECIFIC PRICE EQUATION

Quantifying the effects of both interspecific and intraspecific diversity on a change or difference in total ecosystem function between a baseline and comparison community requires that we combine Equations (1) and (2) (Figure 1). Equation (1) partitions the change in the ecosystem function into different components attributable to changes in interspecific diversity. It is the last term of Equation (1) that we can substitute with Equation (2) to include the effects of intraspecific diversity. This gives

$$\Delta T = \bar{z} \Delta s + \sum_{i=1}^s (w_i - \bar{w})(z_i - \bar{z}) + \sum_{i=1}^s w_i \left(\bar{z}_i \Delta G_i + \sum_{j=1}^{G_i} (w_{ij} - \bar{w}_i)(z_{ij} - \bar{z}_i) + \sum_{j=1}^{G_i} w_{ij} \Delta z_{ij} \right). \quad (4)$$

The terms from left to right on the right-hand side of Equation (4) capture the SRE, the SCE, the IRE, the ICE, and the ICDE. An overview of these five components is also given in Figure 1. Note that the effects of intraspecific diversity can only be calculated for those interspecific groups that are both present in the baseline and comparison communities. For those interspecific groups that are lost, no intraspecific diversity effects can be calculated. Also here, the ICDE of Equation (4) can be

further partitioned using Equation (3), as demonstrated earlier. For a detailed explanation on how to apply the intraspecific Price equation given in Equation (4), we developed hypothetical scenarios and provide detailed calculations of those in Appendix S1: Section S3. In the main text, we apply the method to an experimental study (see section *Application of the method*).

So far, we have focused on extending the interspecific Price equation of Fox (2006), which only captures effects due to losses in interspecific diversity. Similarly, the extended version as given in Equation (4) only captures effects due to losses in intraspecific diversity. An extension that also includes the effects of gains in interspecific and intraspecific diversity, based on the method by Fox and Kerr (2012), is given in Appendix S1: Sections S1 and S2. Briefly, the extended version of the partitioning method of Fox and Kerr (2012) includes nine terms: The first two terms describe the change in total ecosystem function due to a random loss (or gain) of interspecific diversity in the baseline (or comparison) community, the third and fourth term capture the change in ecosystem function due to nonrandom loss (or gain) of interspecific diversity in the baseline (or comparison) community, the fifth and sixth terms describe a random loss (or gain) of intraspecific diversity in the baseline (or comparison) community, the seventh and eighth terms capture the effect of nonrandom loss (or gain) of intraspecific diversity in the baseline (or comparison) community, and the final term captures the ICDE similar to the one given in Equation (4). In the remainder of this study, we refer to Equation (4) as the intraspecific Price equation. As a final note, we would like to point out that the interspecific richness and intraspecific richness loss (resp. gain) effects will always be negative (resp. positive) if interspecific and intraspecific groups have positive functional contributions (i.e., $z_i > 0$ and $z_{ij} > 0$; Fox & Kerr, 2012).

APPLICATION OF THE METHOD

To date, the interspecific Price equation of Fox (2006) has been applied to 129 data sets from both experimental and natural communities worldwide to evaluate the effects of interspecific diversity loss on ecosystem functioning (Genung et al., 2020). Experiments assessing the effect of such loss often focus on the random loss of interspecific groups (i.e., species), in which baseline communities of n interspecific groups are created, and a certain amount of the groups are lost at random in a comparison community. Field studies either use space-for-time substitutions or compare communities that differ at the level of interspecific diversity and ecosystem function (Genung et al., 2020). To apply the extended version of the interspecific

Price equation including the assessment of intraspecific diversity effects, as given in Equation (4), it is necessary to identify (and track) the intraspecific groups of at least one interspecific group in the community at the baseline and comparison community but also to quantify the functional contributions of each of these intraspecific groups. Several studies exist that experimentally manipulated interspecific and intraspecific diversity (e.g., Cook-Patton et al., 2011; Crawford & Rudgers, 2012; Zeng et al., 2017) or that tracked interspecific and intraspecific group abundances (e.g., Hamer et al., 2022; Hattich et al., 2022; Weider et al., 2008). However, to the best of our knowledge, only a few explicitly collected the functional contributions of each of the intraspecific groups that would allow the quantification of the IRE, the ICE, and the ICDE. One such study is that by Weider et al. (2008).

We used the study by Weider et al. (2008) to showcase the applicability of quantifying interspecific and intraspecific diversity effects on ecosystem functioning (here total biomass) using the intraspecific Price equation developed in this study (data used can be found in Govaert et al., 2023). Weider et al. (2008) used three zooplankton species—*Daphnia pulex*, *Daphnia pulicaria*, and their hybrid—which we here designate as distinct interspecific groups. Each of these interspecific groups comprises two genotypes (here representing the intraspecific groups), and these six groups were used to assemble experimental communities that were then exposed to four distinct food quality–quantity treatments, that is, a full-factorial design of low versus high food quality and food quantity (abbreviated as LL, HL, LH, HH). The experiment lasted 90 days, and interspecific and genotype (intraspecific) abundances were measured at Days 30, 60, and 90. While the functional contributions of each genotype were not measured throughout the experiment at each of the specific time points, Weider et al. (2008) did perform a common garden experiment in which size at first reproduction was measured for each genotype in each of the four treatments. Using size, we first calculated the dry weight of each genotype using the length–weight equation for *Daphnia pulex* from Dumont et al. (1975). Assuming that genotypes do not change their functional trait value within the community, we used the size-to-weight transformed values together with the genotype abundance to quantify the biomass of each genotype. Using the biomass of each genotype, we quantified the biomass of each interspecific group for each food condition at each time point by summing the biomass contributions of its genotypes and as a result quantified the total biomass at the community level for each food condition at each time point by summing the biomass contributions of its interspecific groups.

We next wanted to evaluate how much total biomass changes from the community in the low-quality, low-quantity (LL) food environment (here set as our baseline community) to each of the three remaining food environments (here set as our comparison communities). Since the sets of interspecific and intraspecific groups in the comparison communities are not strict subsets of the sets of the interspecific and intraspecific groups in the baseline community, we applied the extended version of Fox and Kerr (2012) (this version is detailed in Appendix S1: Section S1) to the data set. In addition, here in the main text, we only focus on effects in a comparison of the LL food treatment with the high-quality, low-quantity (HL) treatment. The other comparisons and effects are discussed in Appendix S1: Section S4.

At Day 0, we found an increase in total biomass from the LL to HL treatment (Figure 2a). Since at the beginning of the experiment all three species were still present in both treatments at equal abundances, it is not surprising that the increase in the functional contribution to biomass was attributable to the interspecific CDE, which in turn was entirely due to an ICDE. This resulted from a change in the biomass due to a different measured body length of the intraspecific groups in response to the environmental change from low-quality to high-quality food assessed in the common garden experiment (data obtained from fig. 5 in Weider et al., 2008).

At Days 30 and 60, we observed a decrease in total biomass in the HL compared with the LL treatment (Figure 2b,c). For both days, all three interspecific groups were present, so the change in biomass was attributable to an interspecific CDE. However, on both days, within the interspecific groups, one of the genotypes of *Daphnia pulex* was lost. Hence, the interspecific CDE was further partitioned into an intraspecific richness loss effect (IRE_L) and an intraspecific composition loss effect (ICE_L), reflecting the random and nonrandom changes in ecosystem function due to the loss of this genotype. The intraspecific composition loss effect was negative, indicating that the genotype's lost functional contribution was above average. For Day 60, we also lost one of the genotypes of *D. pulicaria*. Based on how the comparison is made here, this reflects a genotype gain comparing the HL to the LL treatment. Indeed, at Day 60, we also obtained intraspecific richness (IRE_G) and composition (ICE_G) gain effects. Finally, for both days we found an ICDE. Regarding effect size, the ICDE contributed most at Day 30 (Figure 2c), whereas the intraspecific richness (IRE_G) and composition gain (ICE_G) effects contributed most at Day 60 (Figure 2c).

Finally, at Day 90, we again observed a decrease in total biomass between the two food quality treatments (Figure 2d). In this case, two entire species were lost in the HL treatment, reflected by the nonzero interspecific

richness (SRE_L) and composition (CDE_L) loss effects. The species lost contributed to the total biomass above average as indicated by the negative interspecific composition loss (CDE_L) effect. We found a positive interspecific CDE, which could be further partitioned into intraspecific richness (IRE_G) and composition (ICE_G) gain effects and an ICDE.

The application of the intraspecific Price equation to the data of Weider et al. (2008) enabled us to dissect the various effects of interspecific and intraspecific diversity and how they contributed to the difference in ecosystem functioning (here total biomass) between two communities differing in food treatment. Effect sizes of the different components provided detailed information on the relative importance of specific interspecific groups and their genotypes. We are convinced that this metric can provide valuable, much more detailed insights into the role of interspecific and intraspecific diversity to changes in ecosystem functioning. To further aid the application of our method, we next discuss suitable experimental designs.

EXPERIMENTAL DESIGNS

Many studies evaluating the similarities and differences between interspecific and intraspecific diversity and their effect on ecosystem functioning (e.g., Cook-Patton et al., 2011; Crawford & Rudgers, 2012; Jiang et al., 2021) use a factorial design in which an interspecific diversity gradient is created by varying the numbers of interspecific groups used and the number of intraspecific groups within one or multiple focal interspecific groups is varied by controlling the number of genotypes or seed families (Figure 3a). Consider, for example, an experimental design in which one varies the number of interspecific groups (here species) from one or two to four species and the seed families within species from one or two to four (e.g., Zeng et al., 2017). In a classical design, all possible combinations are constructed (Figure 3a), and one can assess whether interspecific versus intraspecific diversity has a smaller, equal, or larger effect on the focal ecosystem function of interest. However, such a design in combination with the intraspecific Price equation could also be used to assess the effects of interspecific and intraspecific diversity on change in ecosystem function. For example, using the two-species two-seed-family community as a baseline, one can assess the effects of only interspecific loss and gain (vertical comparisons from the baseline community in Figure 3a), the effects of only intraspecific loss and gain (horizontal comparisons from the baseline community in Figure 3a), or the effects of both interspecific and intraspecific loss and

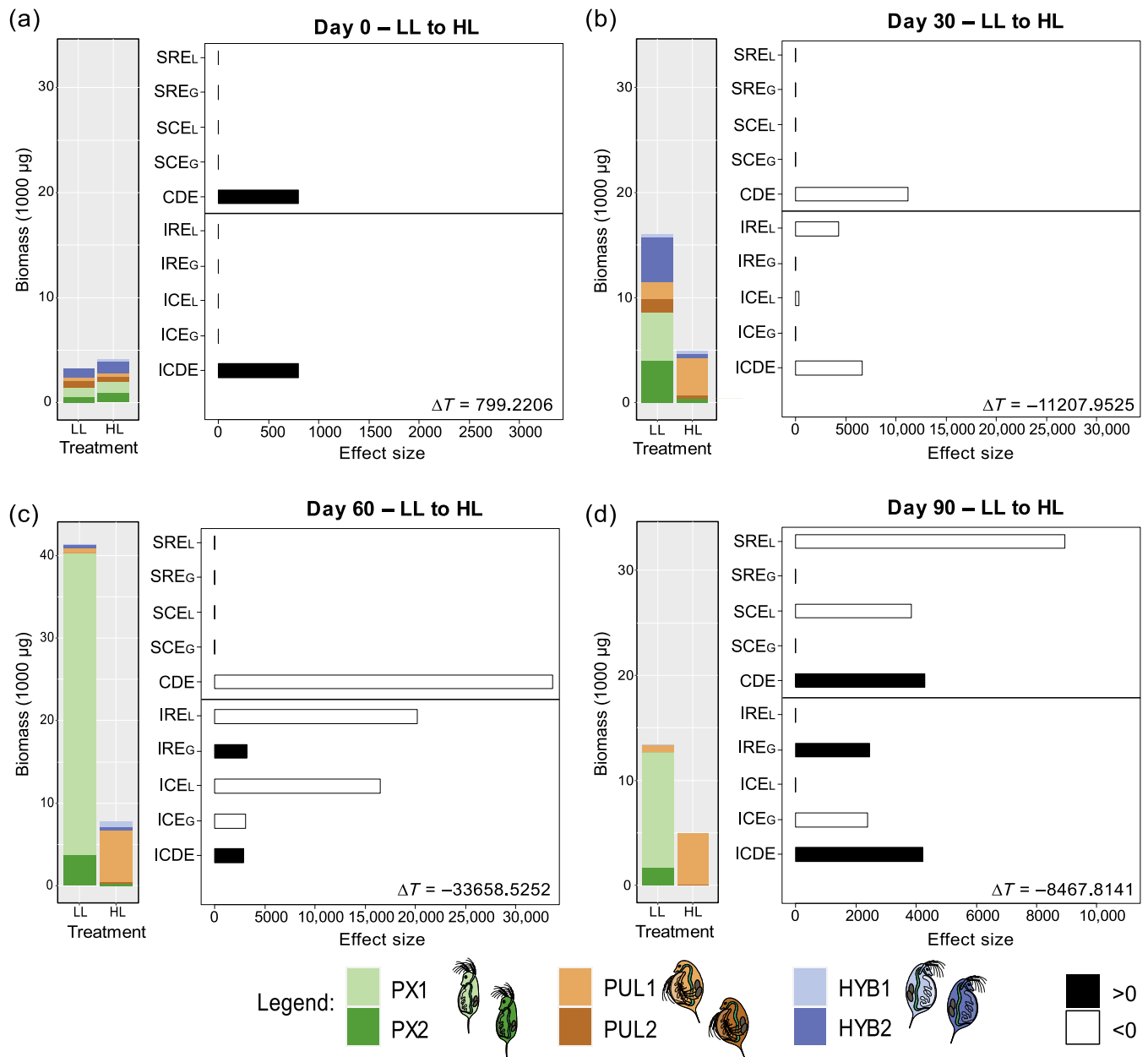


FIGURE 2 Application of intraspecific Price equation to data collected by Weider et al. (2008). Here we illustrate a subset of the data in which we quantify the change in total biomass from the low quality—low quantity (LL) food treatment to the high quality—low quantity (HL) food treatment. Vertical bar charts showcase the biomass of each interspecific and intraspecific group for *Daphnia pulex* (green), *Daphnia pulicaria* (orange), and the hybrid species (purple). Horizontal bar charts indicate the effect sizes of each term of the extended version of Equation (4) given in Appendix S1: Section S1, Equation (S1.4) (>0, filled bars; <0, unfilled bars) calculated at (a) Day 0, (b) Day 30, (c) Day 60, and (d) Day 90. Effect sizes are given for the interspecific richness loss (SRE_L) and gain (SRE_G) effect, the interspecific composition loss (SCE_L) and gain (SCE_G) effect, and the interspecific context-dependence effect (CDE). The latter effect is then decomposed into effects of intraspecific richness loss (IRE_L) and gain (IRE_G) effects, intraspecific composition loss (ICE_L) and gain (ICE_G) effects, and, finally, intraspecific context-dependence effect (ICDE). ΔT reflects the total change in ecosystem functioning. *Daphnia* illustrations by Lynn Govaert.

gain (cross comparisons from the baseline community in Figure 3a). This would make it possible to quantify how each of these qualitatively different losses and gains at different levels of biodiversity impact ecosystem function. In addition, contrasting the losses

or gains at a single diversity level to losses or gains when both levels are included could reveal whether interspecific and intraspecific diversity effects on ecosystem function act additively, antagonistically, or synergistically.

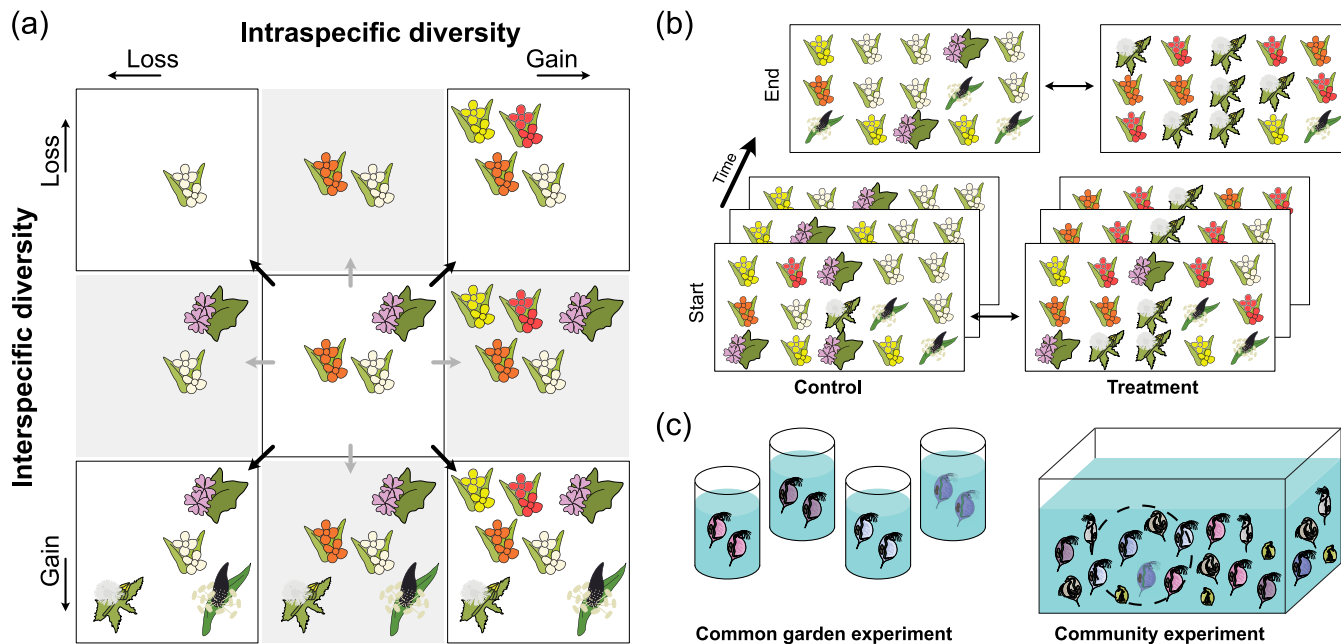


FIGURE 3 Visualization of three experimental designs that could collect the data needed for the intraspecific Price equation (Equation 4). (a) Experimental design varying interspecific and intraspecific diversity. Gray arrows pointing to gray boxes indicate scenarios in which one would measure effects of only interspecific or intraspecific diversity loss or gain, whereas black arrows indicate scenarios in which one would measure the effects of both interspecific and intraspecific diversity. (b) Experimental design in which the same community is exposed to a control and treatment condition. Interspecific and intraspecific diversity effects on change in ecosystem function can be quantified at specific time points (double arrows) or across time (single arrows). (c) Experimental design in which common garden experiments are combined with a community experiment in which abundances of interspecific and intraspecific groups are quantified (e.g., as in the study of Weider et al. [2008]). Plant and *Daphnia* illustrations by Lynn Govaert.

A different set of experiments could involve replicating the same community and exposing these replicated communities to distinct treatments, as we observed in the earlier example by Weider et al. (2008) (but see also Hart et al., 2019; Hattich et al., 2022) (Figure 3b). Weider et al. (2008) also performed a common garden experiment, which provided the necessary information to obtain the functional contributions of each intraspecific group and allowed us to apply the intraspecific Price equation to quantify changes in the total ecosystem function (Figure 3c). Other designs of such an approach can be found in Hart et al. (2019) and Hattich et al. (2022). However, these studies did not provide information on the functional contributions of the intraspecific groups used. If functional contributions of the intraspecific groups had been provided in these studies, then the intraspecific version of the Price equation could have been used to quantify (1) how the absence of evolution impacts ecosystem functioning via a loss of interspecific and intraspecific diversity in Hart et al. (2019) and (2) how increased CO₂ levels affect biomass production via interspecific and intraspecific diversity effects in Hattich et al. (2022). However, in both experiments, no species were

lost. Hence, most likely only an interspecific CDE would have been found, which could then have been further decomposed into intraspecific richness, intraspecific composition, and ICDEs.

Whenever multiple treatments or experimental manipulations are involved, one can quantify how this alters ecosystem functioning via interspecific and intraspecific diversity effects using the control treatment as the baseline community and the treatment conditions as the comparison communities. While such studies could quantify effects across treatments within generations or repeatedly at several time points (as we demonstrated with the study of Weider et al., 2008), one could also track the communities through time and across generations of the species within the communities (Figure 3b). Such designs deliver measurements of ecosystem functional values at consecutive time points across treatments or experimental manipulations, which makes it possible to evaluate the effects of interspecific and intraspecific diversity (1) on changes in ecosystem function across time within communities, (2) between treatments (and, thus, across communities) at several time points, and (3) evaluate how the effects assessed in Item 2 change over time.

FUTURE DIRECTIONS

Here we demonstrated a recursive use of the Price equation by Fox (2006) and Fox and Kerr (2012) to quantify gain and loss effects at both the interspecific and intraspecific levels. Such a recursive property is a well-known feature of the Price equation (Price, 1970, 1972) and has been used to incorporate selection at multiple levels (Arnold & Fristrup, 1982; Okasha, 2006) and to quantify components of trait change at community (Fox, 2006; Fox & Kerr, 2012; Govaert et al., 2016) and ecosystem (Ellner et al., 2011; Genung et al., 2020) levels. While we here focused on ecosystem change quantified as the summed contributions of individual species, the Price equation by Fox (2006) has also been extended to quantify components of richness, composition, and context-dependence to understand changes in community variability (Fox, 2010) and to include total abundance changes rather than the effects of richness per se (Harrison et al., 2022). These methods could also be further extended to include different ecological levels using the recursive property (see Appendix S1: Section S5 for an extension of Harrison et al., 2022). It is clear that the Price equation provides many opportunities to quantify the underlying mechanisms of population, community, and ecosystem change. The intraspecific Price equation presented in this study is one of the many possibilities to extend the “classical” Price equation (Price, 1970, 1972); most likely other combinations are possible depending on the data collected and the research questions asked. Combining versions of the Price equation from evolutionary biology (Queller, 2017), community ecology (Fox, 2006, 2010; Fox & Kerr, 2012), and eco-evolutionary dynamics (Collins & Gardner, 2009; Ellner et al., 2011; Govaert et al., 2016), among others, could provide fruitful avenues to quantify the contributions of different processes to the observed change of interest. To conclude our study, we highlight four future research directions that can be taken using the intraspecific Price equation (Equation 4) to quantify the effects of both interspecific and intraspecific diversity on ecosystem functioning. Importantly, the use of this intraspecific Price equation assumes that one can quantify the functional contributions of both interspecific and intraspecific groups within the focal ecosystems under study. Next, we focus on fruitful future avenues using the intraspecific Price equation method presented in this study.

Quantifying (cor)relations between interspecific and intraspecific diversity effects

A previous meta-analysis by Vellend et al. (2014) found mainly positive correlations between interspecific and

intraspecific diversity (in their study they measured intraspecific diversity as molecular variation within species) when examining the spatial patterns of biodiversity. In addition, experimental studies often demonstrate a positive effect of interspecific and intraspecific diversity on ecosystem functioning (Genung et al., 2020). Given these findings, we might expect a positive correlation between the effects of interspecific and intraspecific diversity on ecosystem functioning. To test this idea, one requires the intraspecific Price equation developed in this study and an experimental design in which one varies the interspecific and intraspecific diversity (e.g., Cook-Patton et al., 2011; Crawford & Rudgers, 2012). Such a design makes it possible to quantify interspecific versus intraspecific diversity loss effects, which can be positively correlated if both types of loss have a positive or negative effect on changes in an ecosystem function of interest (Figure 3a) or negatively correlated if one of the diversity losses has a positive effect while the other one has a negative effect. Most likely, both positive and negative correlations will be found, and this might depend on the ecosystem function of interest. For example, the study by Cook-Patton et al. (2011) showed that increasing interspecific diversity increased aboveground biomass by 16% compared to interspecific monocultures and that this effect was comparable to increasing intraspecific diversity compared to intraspecific monocultures. Here we might expect a positive correlation between the effects of interspecific and intraspecific diversity.

In contrast, Hahn et al. (2017) showed that interspecific diversity (tree species richness in that study) promoted species growth, while intraspecific diversity (seed family diversity in that study) reduced growth. Hence, here we might expect a negative correlation between the effects of interspecific and intraspecific diversity. Positive or negative correlations could occur when different mechanisms with similar or contrasting effects act at the interspecific and intraspecific levels. For example, when interspecific competition affects intraspecific competition (Hamer et al., 2022), increased interspecific competition may reduce intraspecific competition (e.g., Lankau & Strauss, 2008), which may result in contrasting effects of interspecific and intraspecific diversity on ecosystem functioning. Moreover, these correlations do not need to be static but might change depending on the ecosystem state (e.g., competition strengths might change during different stages of community assembly; Kokkoris et al., 1999). In addition, one could also compare the slope of the relation between interspecific and intraspecific diversity effects to a 1:1 line to reveal whether the effects of interspecific versus intraspecific diversity are generally stronger (slope <1) or weaker (slope >1) (e.g., Des Roches et al., 2018).

Assessing the relative importance of interspecific and intraspecific diversity across ecosystem functions and ecosystems

Recent studies have shown that both interspecific and intraspecific diversity are important for and can have equal effects on ecosystem functioning (Des Roches et al., 2018; Raffard et al., 2019). However, it remains unknown whether interspecific and intraspecific diversity impact the same ecosystem functions and whether their contribution varies among ecosystem functions. For example, a study by Pichon et al. (2022) using grassland plant species found no effect of intraspecific trait change on ecosystem functioning (above- and belowground biomass), whereas a study by Raffard et al. (2021) found effects of intraspecific richness in a predator species on several ecosystem functions, such as prey diversity. Hence, the importance of interspecific and intraspecific diversity and their effects may depend on the ecosystem function and even on the ecosystem under consideration. This question could be answered by applying the intraspecific Price equation to many study systems across various ecosystem functions. Meta-analyses similar to those by Des Roches et al. (2018) and Raffard et al. (2019) could then result in distributions of interspecific and intraspecific diversity effects on ecosystem functioning. Organizing these effects across particular groups of ecosystem functions and ecosystems could then reveal idiosyncratic and common patterns of the relative importance of interspecific and intraspecific diversity effects on ecosystem functions.

Identification of large effect groups: Do interspecific groups with large effects harbor intraspecific groups with large effects?

“Keystone species” are species within a community that have a disproportionately large effect on ecological processes compared to their abundance (Paine, 1969). Similarly, studies have identified “keystone genotypes” or “keystone genes” as genotypes or certain genes with a disproportionate large ecological effect compared to their abundance (Barbour et al., 2022; Skovmand et al., 2018). This raises the question of whether interspecific groups with large effects harbor intraspecific groups (or genotypes or genes) with large effects or whether the large ecological effect of an interspecific group is due to the sum of many small effects of its intraspecific groups. However, even when an interspecific group harbors an intraspecific group with a large ecological effect compared to the other intraspecific groups, this interspecific group can still overall have a similar or small ecological effect compared to the

other interspecific groups. Interspecific and/or intraspecific groups with large effects on ecosystem functions can be identified by focusing on the interspecific and intraspecific composition component of the intraspecific Price equation (Equation 4). More specifically, to identify the effect of each group, one can evaluate the specific contributions within the sum components in Equation (4), rather than taking the sum across the interspecific and intraspecific groups. This will allow for comparing effect sizes among interspecific and intraspecific groups and identifying those groups with the largest effects. Interestingly, the importance of interspecific and intraspecific groups might also vary depending on the ecosystem function under consideration. This not only makes it possible to address whether “keystone species” and “keystone genotypes” can have similar effects on ecosystem functioning but also recalls the previous question of where the importance of interspecific and intraspecific groups could vary across different ecosystem functions.

Can intraspecific diversity compensate for interspecific diversity loss?

Many studies have documented similar effects of interspecific and intraspecific diversity on community structure and ecosystem functioning (Des Roches et al., 2018; Raffard et al., 2019). For example, several studies demonstrated similar qualitative and quantitative effects of interspecific and intraspecific diversity of host plant species on arthropod communities (e.g., Cook-Patton et al., 2011; Crutsinger et al., 2006; Johnson et al., 2006), thereby raising the question of whether interspecific diversity can be compensated by intraspecific diversity, or vice versa. Following Des Roches et al. (2021), it seems that intraspecific diversity could partly compensate for interspecific diversity. Indeed, loss of intraspecific diversity could already result in the loss of an ecosystem function even before interspecific diversity loss occurs. However, it remains to be explicitly quantified whether gain of intraspecific diversity within interspecific groups that are not lost can actually offset the loss in ecosystem function due to interspecific diversity loss. A study on microbial communities found that functionally substituting interspecific with intraspecific diversity disrupted interspecific interactions, reducing biofilm formation (Kelvin Lee et al., 2016), suggesting that these two levels might be nonreplaceable. More studies are needed that examine this question, which can be done by combining experimental designs varying interspecific and intraspecific diversity by, for example, substituting the loss of an interspecific group with intraspecific groups among the remaining interspecific groups. Such a design could also

tackle conceptual questions linked to the equivalence of losing one interspecific group versus losing intraspecific diversity across interspecific groups. Then, using the intraspecific Price equation in Equation (4), one could quantify whether the loss of the interspecific group had similar effects on ecosystem functioning compared to the loss of the intraspecific groups among the remaining interspecific groups. Similar to the discussion on “keystone species,” this also raises the question of whether some interspecific groups are more important than others and should be prioritized in attempts to preserve biodiversity (Ellison & Deggrassi, 2017). Studies have referred to these groups as “foundation species” (Dayton, 1972; Ellison et al., 2005). Contrary to keystone species, foundation species have a unique combination of traits and exhibit irreplaceable functions in the ecosystem (Ellison et al., 2005). Can we expect to detect also certain intraspecific groups with a unique set of traits or genes that similarly exhibit irreplaceable functions in the ecosystem?

CONCLUSION: TOWARD A GENOTYPE–ECOSYSTEM APPROACH

While the Convention on Biological Diversity (UN, 1992) recognizes three main levels of biodiversity (intraspecific diversity, interspecific diversity, and diversity between ecosystems), intraspecific diversity and, more specifically, genetic diversity largely remain understudied (O’Brien et al., 2022), even though recognition of their importance and effects on ecosystem functioning is rapidly increasing (Des Roches et al., 2018; Raffard et al., 2019; Stange et al., 2021). This has resulted in increasing interest in measuring and tracking intraspecific diversity over time, with a particular focus on conservation management practices (Czyż et al., 2020; O’Brien et al., 2022; Stange et al., 2021). Additionally, an increasing number of studies is attempting to link genetic data to phenotypic traits to ecosystem functioning (Czyż et al., 2020; Morris et al., 2020; Stange et al., 2021). For example, a study by Morris et al. (2020) proposed to integrate biodiversity–ecosystem research with genotype–phenotype mapping approaches to address how microbial communities change ecosystem functioning. In another example, Czyż et al. (2020) used imaging spectrometer data from tree canopy to connect spectroscopy data to genetics data, illustrating the potential to detect genotype-specific phenotypic features in spectral reflectance data in a natural forest. Future applications may also involve a better connection between eDNA approaches, morphological measurements, and

genetics data to quantify allele frequencies at the trait-relevant loci linking intraspecific groups to their functional contribution in the ecosystem. From these studies, and with ever-growing technological advances, it is clear that we are progressing toward a true gene-to-trait-to-ecosystem function approach, in which simply knowing which genes or genotypes are present will make it possible to predict intraspecific traits and quantify ecosystem functioning. In such a setting, methods like the intraspecific Price equation, as presented in this study, that connect the effects of different diversity levels on ecosystem functioning will be most useful in terms of providing additional information on how losses or gains in these diversity levels impact ecosystem functioning.

AUTHOR CONTRIBUTIONS

Lynn Govaert conceptualized the study, performed data analyses, and wrote a first draft of the manuscript with input from Andrew P. Hendry, Farshad Fattahi, and Markus Möst. All authors contributed to subsequent revisions of the manuscript.

ACKNOWLEDGMENTS

Lynn Govaert is funded by the Deutsche Forschungsgemeinschaft (DFG, Project 511084840). We would like to thank two anonymous reviewers for their constructive feedback on the manuscript. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Govaert et al., 2023a) are available in Dryad at <https://doi.org/10.5061/dryad.r4xgxd2jf>. R code (Govaert et al., 2023b) is available in Zenodo at <https://doi.org/10.5281/zenodo.7827593>.

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SUPPORTING INFORMATION

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

How to cite this article: Govaert, Lynn, Andrew P. Hendry, Farshad Fattahi, and Markus Möst. 2024. "Quantifying Interspecific and Intraspecific Diversity Effects on Ecosystem Functioning." *Ecology* 105(1): e4199. <https://doi.org/10.1002/ecy.4199>