

Relationships between ecosystem functions are temporally variable and driven by plant species richness and plant community composition

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Abstract

Ecosystem management aims at providing many ecosystem services simultaneously. Such ecosystem multifunctionality can be limited by trade-offs and increased by synergies among the underlying ecosystem functions (EF), which need to be understood to develop targeted management. Previous studies found differences in the correlation between EFs. We hypothesised that correlations between EFs are variable even under the controlled conditions of a field experiment and that seasonal and annual variation, plant species richness, and plot identity (identity effects of plant communities such as the presence and absence of functional groups and species) are drivers of these correlations. We used data on 31 EFs related to plants, consumers, and physical soil properties that were measured over 5 to 19 years, up to three times per year, in a temperate grassland experiment with 80 different plots, constituting six sown plant species richness levels (1, 2, 4, 8, 16, 60 species). We found that correlations between pairs of EFs were variable, and correlations between two particular EFs could range from weak to strong correlations or from negative to positive correlations among the repeated measurements. To determine the drivers of pairwise EF correlations, the covariance between EFs was partitioned into contributions from plant species richness, plot identity, and time (including years and seasons). We found that most of the covariance for synergies was explained by species richness (26.5%), whereas for trade-offs, most covariance was explained by plot identity (29.5%). Additionally, some EF pairs were more affected by differences among years and seasons and therefore showed a higher temporal variation. Therefore, correlations between two EFs from single measurements are insufficient to draw conclusions on trade-offs and synergies. Consequently, pairs of EFs need to be measured repeatedly under different conditions to describe their relationships with more certainty and be able to derive recommendations for the management of grasslands.

ABSTRACT

Ecosystem management aims at providing many ecosystem services simultaneously. Such ecosystem multifunctionality can be limited by trade-offs and increased by synergies among the underlying ecosystem functions (EF), which need to be understood to develop targeted management. Previous studies found differences in the correlation between EFs. We hypothesized that correlations between EFs are variable even under the controlled conditions of a field experiment and that seasonal and annual variation, plant species richness, and plot identity (identity effects of plant communities such as the presence and absence of functional groups and species) are drivers of these correlations. We used data on 31 EFs related to plants, consumers, and physical soil properties that were measured over 5 to 19 years, up to three times per year, in a temperate grassland experiment with 80 different plots, constituting six sown plant species richness levels (1, 2, 4, 8, 16, 60 species). We found that correlations between pairs of EFs were variable, and correlations between two particular EFs could range from weak to strong correlations or from negative to positive correlations among the repeated measurements. To determine the drivers of pairwise EF correlations, the covariance between EFs was partitioned into contributions from plant species richness, plot identity, and time (including years and seasons). We found that most of the covariance for synergies was explained by species richness (26.5%), whereas for trade-offs, most covariance was explained by plot identity (29.5%). Additionally, some EF pairs were more affected by differences among years and seasons and therefore showed a higher temporal variation. Therefore, correlations between two EFs from single measurements are insufficient to draw conclusions on trade-offs and synergies. Consequently, pairs of EFs need to be measured repeatedly under different conditions to describe their relationships with more certainty and be able to derive recommendations for the management of grasslands.

Keywords

Correlation analysis; Synergies; Trade-off; Biodiversity; Temporal Variability; Ecosystem function relationships

INTRODUCTION

Land management and policy aim to improve human well-being by providing multiple ecosystem services, i.e., ecosystem multifunctionality (Dade, Mitchell et al. 2018). The Millennium ecosystem assessment (2005) defined ecosystem services (ES) as the 'benefits people obtain from ecosystems', e.g., food, water, timber, and cultural values. Ecosystem services derive from ecosystem functions (EF) (Balvanera, Pfisterer et al. 2006, Costanza, de Groot et al. 2017), which describe the biogeochemical processes that are influenced by the organisms and their traits to sustain an ecosystem (Millennium ecosystem assessment 2005, Reiss, Bridle et al. 2009). These ecosystem functions can be used to measure the flow and exchange of materials and energy in ecosystems directly (Naeem 1998), or indirectly via ecosystem properties, such as storage and retention of water or nutrients (Costanza, de Groot et al. 2017). In the last decades, the average global crop yields have been rising due to more intensive management practices in agriculture (Foley, Ramankutty et al. 2011). These management practices had negative side effects on the environment, such as declines in native pollinators, and increases in pests and diseases, degrading land and water (Gordon, Peterson et al. 2008, Foley, Ramankutty et al. 2011). On the other hand, one important aim of nature conservation is to protect areas in order to preserve important ES, such as carbon sequestration and climate regulation, and to avoid widespread biodiversity declines (Watson and Venter 2017). While ES multifunctionality may be an implicit or explicit management aim, current management strategies often focus on providing single ecosystem services, e.g., maximising productivity or the value for nature conservation. ES multifunctionality requires EF multifunctionality (Manning, van der Plas et al. 2018). Since many ecosystem functions improve with increasing plant species richness (Scherber, Eisenhauer et al. 2010, Weisser, Roscher et al. 2017), diversifying ecosystems has been proposed as an alternative management target, and studies have found a generally positive relationship between plant species richness and multifunctionality (Cardinale, Srivastava

et al. 2006, Gamfeldt, Hillebrand et al. 2008, Pasari, Levi et al. 2013, Dooley, Isbell et al. 2015, Finney and Kaye 2017, Hautier, Isbell et al. 2018, Meyer, Ptacnik et al. 2018).

One challenge of promoting multifunctionality is that the simultaneous enhancement of all EFs is likely impossible because there are trade-offs between EFs (Rodríguez, Beard Jr et al. 2006, Manning, van der Plas et al. 2018, Meyer, Ptacnik et al. 2018). Such trade-offs occur when the provisioning of one EF improves at the expense of another EF. For example, under conventional management of single crops, high productivity often is associated with soil degradation (Kleinman, Sharpley et al. 2011, Pereira, Bogunovic et al. 2023). In contrast, synergies among EFs occur when EFs are co-varying in the same direction (Rodríguez, Beard Jr et al. 2006). For example, high below-ground biomass production is related to a high below-ground carbon storage (Hanisch, Schweiger et al. 2020).

Two mechanisms can cause correlations between EFs. The first mechanism consists of common drivers affecting multiple EFs (Bennett, Peterson et al. 2009), referred to as the common-driver-mechanism in the following. Environmental conditions can improve one EF while deteriorate another EF (Bradford, Wood et al. 2014), thereby causing a trade-off between the two EFs or a synergy if both EF would improve or deteriorate in the same way in response to the environmental condition. For example, Maestre, Quero et al. (2012) found that an increase in temperature decreased multifunctionality, which could indicate that either individual EFs are negatively affected by increasing temperature, or that higher temperature can cause weaker synergies and/or stronger trade-offs among EFs. The second mechanism consists of physiological or ecological constraints among EFs (Bennett, Peterson et al. 2009), referred to as ecological-constraints-mechanism in the following. As resources are limited within an ecosystem, not all EFs can be improved simultaneously, independent of external drivers. Carbon sequestration, for example, can be enhanced by afforestation, but during tree growth, evapotranspiration is increased, and water availability deteriorated (Engel, Jobbágy et al. 2005). Management strategies cannot easily overcome ecological constraints. Consequently, correlations among EFs need to be understood to mitigate trade-offs and enhance synergies (Shen, Li et al. 2020). One decision strategy for ecosystem management could be to consider the occurring species traits to avoid potential trade-offs, as species traits link EFs with each other (Hanisch, Schweiger et al. 2020). An attempt to consider species traits is to maximize the number of species present, as each species possesses a large number of traits, or to consider functional groups, classifying groups of plant species according to plant traits, which seem more likely to influence EFs (Tilman 2001, Roscher, Schumacher et al. 2004). Consequently, correlations among EFs and the underlying drivers need to be understood to mitigate trade-offs and enhance synergies (Shen, Li et al. 2020), which is essential to manage ecosystems for multifunctionality.

For example, for the EF-classes 'Nutrition biomass' and 'Life cycle maintenance, habitat and gene pool protection', as many as 50-75% of the case studies reported a trade-off, whereas 25-50% reported a synergy or no relationship between these classes. For the EF classes 'Intellectual and representative interactions' and 'Physical and experiential interactions', 50-75% of the studies reported synergies, while 25-50% reported the opposite or no relationship. The underlying causes of these conflicting results are still subject to debate (Dade, Mitchell et al. 2018).

There are several possibilities why the relationship between two particular EFs could differ among studies. First, the relationship between EFs can change based on the scale or land system considered, e.g. urban area vs. agricultural area (Adhikari and Hartemink 2016, Lee and Lautenbach 2016). Second, most studies investigated EF relationships based on single measurements. However, ecological drivers, such as diversity or nutrient availability, can change over time and cause variation in relationships between EFs (Crouzat, Mouchet et al. 2015, Torralba, Fagerholm et al. 2018, Zheng, Wang et al. 2019). Third, differences in the ecosystem investigated, or in abiotic conditions among sites, can cause variation regarding EF relationships among studies. Land-use type (Li, Chen et al. 2018), management intensity (Rodríguez, Beard Jr et al. 2006), and environmental factors like climate and soil pH have been shown to strongly affect individual EFs (Wang, Liu et al. 2021), and the correlations between EFs (Spake, Lasseur et al. 2017). If these drivers affect EFs differently, a change in the driver will change the relationship between these EFs. One example would be EFs dependent on water availability, such as shoot length and root length, being positively related

within a year of high precipitation (Pérez-Ramos, Roumet et al. 2012), and showing a weaker relationship at low precipitation, when plants invest more in roots than shoots (Mokany, Raison et al. 2006). In addition, previous studies have found that drivers of individual EFs are of different importance at different places and time points (Isbell, Calcagno et al. 2011, Crouzat, Mouchet et al. 2015, Torralba, Fagerholm et al. 2018, Zheng, Wang et al. 2019, Martin, Durand et al. 2020, Shen, Li et al. 2020, Willemsen 2020). This implies that also the variability in EF relationships may differ among places and time points as these drivers can influence EF relationships directly by changing the ecological dependency of the two EFs or indirectly by affecting EFs individually and therefore causing a change in their covariance. Finally, also differences in the statistical methods used to evaluate relationships between EF classes can bias results (Lee and Lautenbach 2016). For example, no-effect relationships were more likely to be found when correlation coefficients were used, whereas descriptive methods such as GIS-analyses, which quantify and describe EF relationships based on cooccurrence of EF at the same location, showed a higher probability to identify trade-offs (Lee and Lautenbach 2016). In summary, there are several reasons why relationships between different EFs may vary. Whereas a few studies recorded the variation of individual EFs (van der Plas, Schröder-Georgi et al. 2020) and their drivers over time (Gaglio, Aschonitis et al. 2020, van der Plas, Schröder-Georgi et al. 2020), such studies are lacking for EF relationships.

To understand whether EF relationships are inherently variable or whether meta-analyses detected variability because of differences among studies, studies investigating EF relationships repeatedly under comparable conditions are needed. Furthermore, the drivers of EF relationships need to be investigated to understand, what might cause variability in EF relationships. Drivers and variability of EF relationships might depend on the individual EFs or their proxies investigated. For example, it was shown, that plant diversity has particularly strong effects on lower trophic levels and effects dampen with increasing trophic levels (Scherber, Eisenhauer et al. 2010). Consequently, it can be expected, that EFs depending on different components of the ecosystem (e.g. plant productivity and soil microbes) show different EF relationships or a higher variability of EF relationships. Furthermore, we expect to see similar EF relationships between EFs depending on the same components of the ecosystem, e.g. between EFs representing plant productivity and EFs representing invasion resistance.

Here we used data of 31 EFs repeatedly measured during 5 to 19 years in a large-scale temperate grassland biodiversity experiment, i.e., the Jena Experiment (Roscher, Schumacher et al. 2004, Weisser, Roscher et al. 2017). The 31 EFs covered different components of the ecosystem related to plant productivity, plant nutrients, soil microbes, consumers, invasion resistance, soil properties, and soil nitrogen and carbon concentrations, which are called classes of EFs hereafter. Our study aimed to systematically investigate the variability in the pairwise relationships between EFs and the underlying drivers of variability. Specifically, we addressed the following questions:

- (1) How variable are EF relationships over time? Do pairs of EFs differ in their relationship between replicated measurements?
- (2) What drives the relationship among EFs? How much do years, seasons, species richness and the identity of the plots (representing the identity of the studied plant communities) contribute to these relationships by affecting pairs of EFs in similar or opposing ways?
- (3) Are synergies and trade-offs driven differently by years, seasons, plant species richness and the identity of the studied plots?

METHODS

Study site

In 2002, the Jena Experiment, a biodiversity experiment with 82 plots was established at a former arable field near to the city of Jena (Germany) (Roscher, Schumacher et al. 2004, Weisser, Roscher et al. 2017). The plots were sown in May 2002 with a species richness (SR) of 1, 2, 4, 8, 16 and 60 grassland plant species,

with 16, 16, 16, 16, 14 and 4 replicates, respectively (each replicate was a unique species composition, i.e. community, except for the highest richness level where all replicates had the same species composition). Plot identity ("plot ID") represents the different plots containing different plant communities with a variety of compositional features (Jochum, Fischer et al. 2020). Plant species for communities with 1–16 species were randomly chosen from a pool of 60 plant species typical for *Arrhenatherum* grasslands with restrictions to create different levels of functional-group richness within each level of species richness. We distinguished three functional groups, namely grasses, herbs (small herbs and tall herbs combined), and legumes, based on ecologically relevant attributes (Roscher, Schumacher et al. 2004). Species richness and functional group richness (FGR), number of functional groups per community) were varied as independently as possible (Roscher, Schumacher et al. 2004). All plots were mown twice a year, did not receive any fertiliser, and were weeded two to three times a year (Roscher, Schumacher et al. 2004). The chosen mowing regime corresponds to the region's typical management of extensively used hay meadows (Weisser, Roscher et al. 2017). Two monocultures were given up due to the weak establishment of the target species in the first years, resulting in 80 plots used for this analysis.

Dataset

We based this analysis on 31 EFs measured during 5 to 19 years in the Jena Experiment (full description in Supporting Information A, Table S1). These EFs are indicative of eight classes of EFs: plant productivity, plant nutrients, soil microbes, consumers, invasion resistance, soil carbon, soil nitrogen, and soil properties (Table 1). The EFs within one class of EFs are often related.

The data were categorised into spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February) according to the meteorological seasons of the Northern Hemisphere. In the case of multiple measurements of the same EF per season and year, the raw data were averaged per plot, year, and season. The EFs were always measured on all plots but in different numbers of years and seasons. The number of years ranged from 5 to 19, and most EFs were measured once or twice a year. A dataset comprising all plots is referred to as a measurement in the following. The number of measurements ranged from a minimum of 5 (SoilDensity) to a maximum of 36 (PlantHeight). The inverse of some EFs was used to represent a valuable function according to humans' perspective enabling to identify synergies and trade-offs (Table 1).

Table 1: List of all Ecosystem functions (EF), the classes of EFs they represent, the abbreviations for the EFs used in the f

Class of EF

Consumer

Invasion resistance

Plant productivity

Plant nutrients

Soil carbon

Soil microbes

Soil nitrogen

Soil properties

Data preparation

All data manipulations and later analyses were conducted using the free software R 3.6.2 (R Core Team 2019) and Rstudio 1.1.442 (RStudio Team 2016). To approximate normal distributions, all raw data (EF_{raw}) were boxcox-transformed (EF_{boxcox}) using two lambda-values (λ and λ_2) estimated with the package "geoR" (Ribeiro Jr 2020):

$$EF_{boxcox} = \text{boxcoxtransformed} (EF) = \frac{E\Phi_{\rho\alpha\omega} + \lambda_2^{\lambda} - 1}{\lambda_2^{\lambda}}$$

english λ

To scale all EFs to a comparable range of 0 to 1, the EF_{boxcox} were minmax-transformed (EF_{minmax}):

$$EF_{minmax} = \text{minmaxtransformed} (EF) = \frac{EF_{boxcox} - \min(EF_{boxcox})}{(\max(EF_{boxcox}) - \min(EF_{boxcox}))}$$

Variation in individual EFs

The variation of individual EFs was quantified as a standard deviation over all data points (individual measures on plots). The individual EFs are often measured at the same time (Supporting information A, Table S2). Thus, variation of individual EFs is expected to be comparable and not biased by the identity of years and seasons measurements were taken. However, we tested whether the variation of individual EFs depended on the number of repeated measures, meaning how often in time EFs were measured (number of years * number of seasons). Therefore, a model with the standard deviation per individual EF depending on the explanatory variable "number of repeated measures" (number of years * number of seasons an individual EFs was measured) was run.

The drivers of the variation in individual EFs (EF_{minmax}), were tested in a linear model with the explanatory terms "block" (factor with four levels), "SR" (initial number of species planted, log-transformed continuous variable), "plotID" (factor with 80 levels), "season" (factor with 3 levels, as no measurements were done in winter), "year" (continuous variable), and their interactions. The plot identity (plotID) effect mainly accounts for differences among the initially planted communities. This set of terms is referred to as "drivers" in the following. The same model was conducted for EFs measured only once per year excluding "season" and the respective interaction terms.

To analyse whether different classes of EFs were affected differently by drivers, the variance in individual EFs explained by individual drivers was calculated by dividing the sum of squares explained by the driver by the total sum of squares in the respective model of the individual EFs explained above. In a subsequent model the explained variation per EF and per driver were used as meta-data. The variation was tested against the classes of EFs (with the different classes of EFs as levels) and the drivers (with the levels "block", "SR", "plotID", "season", "year", and their interactions) as independent variables.

Relationships between pairs of EFs

Relationships between EF pairs were statistically investigated using covariances and correlations. In correlations, the relationship between two EFs was standardised by the variation of the individual EFs (product of their standard deviations), enabling us to compare relationships between different EF pairs. To calculate correlation coefficients, we used the R-package Hmisc 4.4-2 (Harrell Jr 2020). We used the non-standardised relationships (covariances) to analyse the influence of drivers on relationships among EFs.

Variation in EF correlations

To quantify the general strength and variation of EF correlations, we calculated the mean and the standard deviation of Fisher's Z-transformed correlation coefficients for each EF pair. Correlation coefficients were calculated among measurements on all plots at a particular time point and then averaged across time points. Hence we refer to this correlation as the mean correlation. It includes the effects of species richness and plot identity. In order to plot the EF relationships as correlation coefficients on a scale of -1 (perfect negative) to 1 (perfect positive correlation), the mean correlation coefficients were back-transformed from Z-scale.

The standard deviation of the individual correlations at the different time points quantifies the temporal variation (among seasons and years) of correlations among EFs. However, using all time points to calculate the temporal variation, might be influenced by the number of time points and the identity of time points (deviating years or seasons). Therefore, first, we checked whether this temporal variation, based on all time points, depended on the number of time points. We analysed the temporal variation of the correlations per EF pair as a function of the number of timepoints that EF pair was measured (number of years* number of seasons). The number of repeated measures for pairwise EFs, meaning the number of times two EFs were measured at the same time (same year and same season), ranged from 0 to 36 times (Supporting information B, Table S2 contains an overview of the individual EFs and at what time (years and seasons) they were measured). Second, we checked whether the variation of correlations per EF pair depended on the identity of the time point that EF pair was measured. Therefore, for each EF-pair we randomly chose four time points to calculate a standard deviation of the respective correlation coefficients. For each EF-pair this was done 20 times. The range of these 20 standard deviations per EF pair was used to check whether the standard deviation for that EF pair was stable (small range indicating no identity effect of years and seasons) or not (large range indicating strong identity effects of years or seasons).

Drivers of the covariance between EF pairs

To analyse whether years, seasons, species richness, and plot identity affect EF relationships by driving individual EFs in similar or opposing ways, we partitioned overall covariances into contributions of the different explanatory terms. Here, plot identity was further decomposed in the effects of functional group richness, and the presence of the functional groups legumes, herbs (tall and short herbs combined), or grasses. This decomposition of covariances was based on an additive partitioning of sums of products (SPs) in the same way as additive partitioning of sum of squares (SS) is used in a decomposition of variances in an analysis of variance (ANOVA). This type of covariance analysis has previously been used to investigate, for example, the influence of explanatory terms on trait-trait relationships (He, Wang et al. 2009) and is frequently used in quantitative genetic and phylogenetic approaches (Kempthorne 1957, Bell 1989).

The sums of products, which are equivalent to covariances, were obtained per EF pair using the following

formula:

$$SP(X, Y) = \frac{SS(X + Y) - SS(X) - SS(Y)}{2}$$

where X and Y are the EFs of interest, and X+Y is the sum of the two EFs. The SS were obtained from general linear models (implemented with the `lm()` function in R (Mangiafico 2015)) with the explanatory terms "block", "log(SR)", "plotID", "season", "year", and the interactions "season:year", "log(SR):(season + year + season:year)", "plotID:(season + year + season:year)" (note that here, following conventions of R, we use the colon instead of a multiplication sign as interaction operator). For each EF pair, three linear models were run: one for each of the individual EFs (X and Y) and one for the sum of the two EFs (X + Y), based on the measurements from different time points of EF_{minmax}. Like in ANOVA, SPs are divided by their degrees of freedom to obtain mean SPs (MSPs), which are divided by residual MSP to calculate F-ratios and significances. Because there are nested effects, not all terms could be tested against "Residuals". "Block" and "log(SR)" had to be tested at the level of variation between plots with different species compositions (plotID). Similarly, the interaction terms "log(SR):(season + year + season:year)" had to be tested for the same reason against "plotID:(season + year + season:year)". All other terms were tested against "Residuals" (Supporting Information B, Table S3). It has been shown that for balanced experimental designs such as the Jena Experiment this method is comparable to linear mixed-model analysis using restricted maximum likelihood methods (Schmid, Baruffol et al. 2017).

Because SPs are additive, we can express the influence of each driver on EF covariation (i.e., the relationship between the EFs) by calculating the percentage of the (absolute) total sum of products explained, similar to a percentage variance explained (He, Wang et al. 2009). However, unlike variances, covariances are either positive, indicating a positive relationship between two variables, or negative, indicating an inverse (i.e. trade-off) relationship between two variables. The sign of SPs for each explanatory term informs us about whether covariances are positive or negative. This means that we could deduce whether the individual drivers affected the EFs in a pair in an trade-off (negative covariance) or synergistic (positive covariance) way. Therefore, we show "signed percentages" of covariance in the results by multiplying the absolute percentages with the sign of the respective covariance.

RESULTS

Variation in individual EFs

First, we compared the variation of individual EFs and EF classes. The average standard deviation, calculated by averaging all standard deviations of all EFs, was 0.17. While some EFs varied strongly in time among replicated measures, other EFs showed a low variation (Table 2; minimum standard deviation was 0.07 for plant carbon, maximum standard deviation was 0.38 for plant sodium). The variation of individual EFs did not depend on the number of times (number of years * number of seasons) they were measured ($F_{1,29} = 0.753$, $p = 0.393$) (Supporting information C, Fig. S3). Classes of EFs did not differ significantly in their variation ($F_{7,23} = 0.76$, $p = 0.63$; Table 2).

Table 2: Variation in ecosystem functions (EF) expressed as standard deviation. The standard deviation over all measurements

Classes of EF

Consumer

Invasion resistance

Plant productivity

Plant nutrients

Soil carbon

Soil microbes

Soil nitrogen

Soil properties

Second, we tested if measures of individual EFs differed among years, seasons, species richness levels, and plot identities (Fig. 1). Considering all EFs, year explained on average 4.7% of the variation of EFs, and season explained on average 4.1%. Additionally, species richness explained 8.6%, while plot identity explained 21.3% of the variation of individual EFs. These differences explained about one-fourth of the variation of the individual EFs. One-third of the variation in individual EFs was unexplained: 34.1% for EFs, which were measured in several seasons, and 48.3% for EFs measured in just one season. All tested interaction terms explained only a small part of the total variation of the EFs (Fig. 1).

Different variables explained the variation of EFs in different classes of EFs. For example, for invasion resistance and plant productivity, SR explained a large proportion of the variation (on average, 23.1% and 21.0%; Fig. 1, green). For consumer-related functions, year explained a large proportion (on average 11.9%; Fig. 1, red). For plant nutrients, plot identity explained, on average, 38% of the variation (Fig. 1, blue). This means, that classes of EFs were differently affected by biological and environmental conditions (classes of EF: $F_{7,245}=4.2$, $p<0.01$; Driver $F_{12,245}=38.35$, $p<0.01$; classes of EF: Driver: $F_{60,245}=5.4$, $p<0.01$, where "driver" represents the year, season, SR, plotID and their interactions).

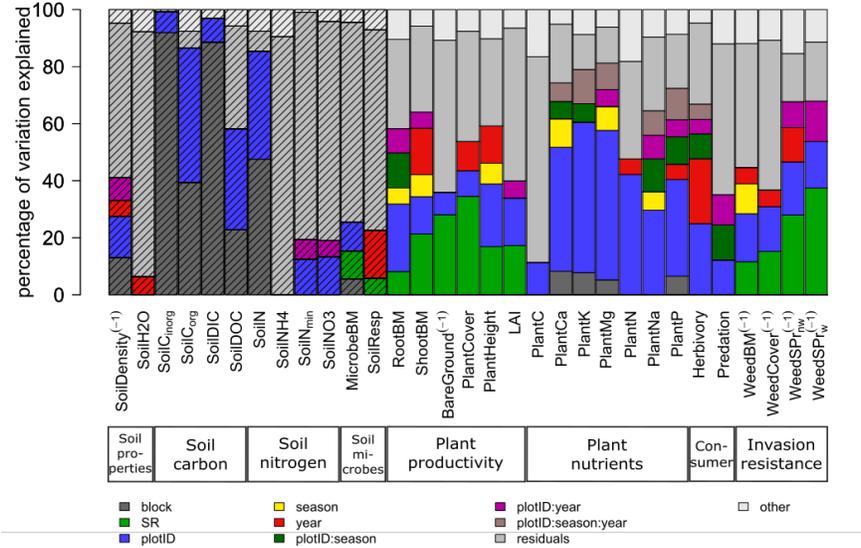


Figure 1: Percentage of variation in individual EFs that was explained by year, season, species richness (SR), plot identity (plotID), and the interaction among these variables. The influence of the explanatory terms is plotted in % of total sum of squares, corresponding to increments in multiple $R^2 * 100$. Explanatory terms are plotted for individual effects $> 5\%$. All effects less $< 5\%$ are summarized as "other", e.g. various interaction-effects. Hatched barplots represent a simpler model, including only year, SR, plotID and their interactions for EF, which were measured in only one season. Non-hatched barplots represent full models including all terms. The graph corresponds to a hierarchical partitioning of type one (Groemping 2006), but because explanatory terms were not correlated, there was no need to average across different fitting sequences.

Variation in EF correlations

Positive correlations (indicating synergies) and negative correlations (indicating trade-offs) were observed across all measures (Fig. 2, upper triangle). For instance, plant height and shoot biomass showed a synergy, while soil dissolved carbon and plant height showed a trade-off in their mean correlations. The strength of these correlations differed among pairs of EFs, with some EF pairs showed no correlation, while others showed weak, moderate, or strong correlations. We observed no strong negative correlations. All EFs showed positive correlations to some and negative correlations to other EFs (according to their mean correlation) (Fig. 2, upper triangle), with EFs in some classes showing predominantly positive correlations (plant productivity and invasion resistance) and others mostly negative correlations (plant productivity and plant nutrients). The EF correlations were robust against the method of calculating correlations, i.e. whether we used mean correlations (correlation coefficient averaged across time points), grand-total correlations (one correlation coefficient using all data from all time points), or between-group correlations (one correlation coefficient calculated with datapoints averaged across time points) (Supporting information D, Fig. S4). As expected, EF correlations tended to be stronger when the variation of individual measurements across time points was removed, i.e. for the between-group correlations (Supporting information D, Fig. S4).

The variation per EF pair was quantified by the standard deviation of correlation coefficients, which were calculated for every time point when the two EFs were measured in the same year and season. Overall, there was considerable variation in EF correlations (mean standard deviation = 0.16, mean correlation coefficient = 0.14) (Fig. 2, lower triangle). We tested if the variation in the EF correlations depended on the correlation's average strength. EF pairs generally showed a higher variation in their correlation when they show a stronger correlation irrespective of this correlation being positive or negative ($F_{5,281}=9.4$,

$p < 0.001$, Supporting information E, Fig. S5). Additionally, we tested if the variation in the EF correlations depended on the number of times the EF-pair was measured (number of years * number of seasons). EF pairs generally showed an increasing variation in their correlations with a higher number of times the EF-pair was measured ($F_{1,572} = 120.91$, $p < 0.001$) (Supporting information E, Fig. S6). Lastly, we checked whether the variation in correlations among EFs depend on the identity of time points they were measured. These ranges of temporal variation were rather small, on average showing a standard deviation ± 0.08 (Supporting information D, Fig S7). Furthermore, the range of temporal variation of correlations, are different for the individual EF-pairs, some EF-pairs show a strong identity effect of time points (e.g. SoilNH4...SoilN_{min}, PlantCover...WeedCover) and some a weak identity effect of time points (e.g. ShootBM...SoilN, PlantC...SoilC_{org}) (Supporting information E, Fig S7).

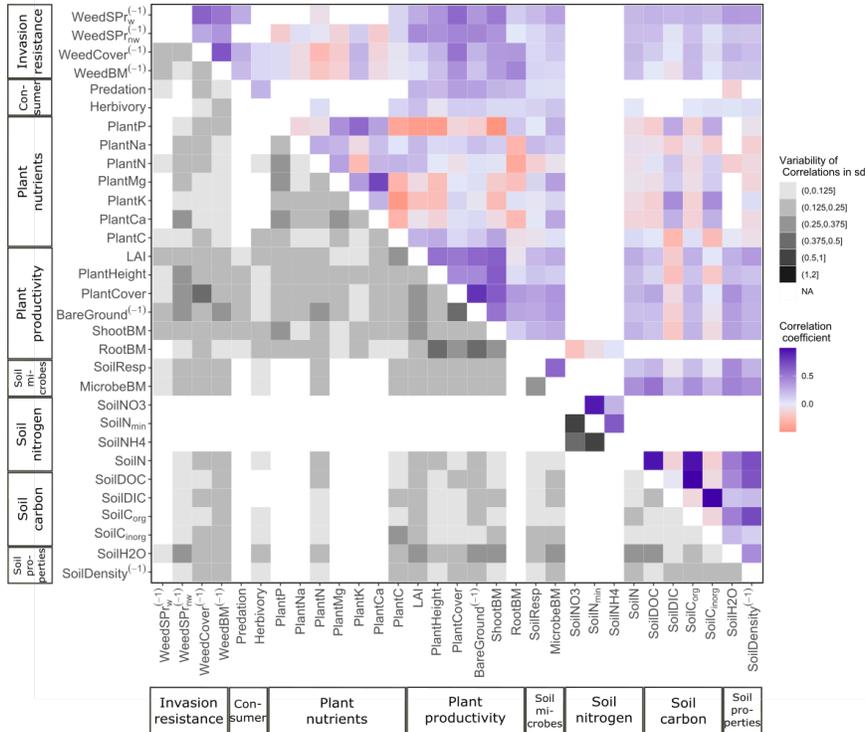


Figure 2: Variation in the correlations between pairs of ecosystem functions (EFs) (lower triangle) and average correlation between these EFs (upper triangle). The different EFs (see list in table 1) were grouped into classes. Mean correlations were calculated using Fisher’s Z transformation of EF correlations per season and year that were averaged over time. The standard deviation of the EF correlations per year and season was calculated to estimate the variation of EF correlations. When no average correlation is shown, the respective EF was not measured in the same season and year. A missing standard deviation for an EF pair shown to have a correlation coefficient represents cases where a correlation coefficient could only be calculated for a single time point.

Drivers of the covariance of EF pairs

To test if the drivers year or season, species richness, and plot identity affect relationships among EFs, we quantified the covariance between all pairs of EFs and the contribution of each driver to these covariances in percentage. These percentages were signed because the drivers can contribute to the EF covariances by affecting the underlying EFs synergistically (signed positive) or antagonistically (signed negative). Importantly, the contribution of individual drivers can have antagonistic (more negative covariance) or synergistic

(more positive covariance) effects irrespective of the overall relationship between the respective EF being a synergy or a trade-off.

All tested drivers (year, season, SR, and plot ID) affected the covariances between EFs. The largest fraction of covariance among EFs was explained by SR and plotID. However, effects differed between EF pairs in synergies and trade-offs (defined by the sign of the mean correlation, Fig. 2, upper triangle). For synergies, most of the covariance was explained by SR (26.5%). In contrast, for trade-offs, most of the covariance was explained by plot identity (-29.5%, Fig. 3), with the negative value indicating that the individual EFs were driven antagonistically, causing a trade-off. When further investigating plotID, the presence of herbs and legumes already explained half of the effect of plot ID (Supporting information F, Table S4). For synergies, plot ID had intermediate positive effects (18%), mainly due to the presence of grasses and herbs. Year and season caused both positive and negative covariances, so that the average percentages explained by year and season were low (2.8% and -0.6%). For trade-offs, the average percentage of explained covariance by SR was low (-4.2%), contributing positively and negatively to covariance. Season contributed an additional -12.1% to covariance, while year explained very little (-1.3%). Interactions between drivers explained very little covariance (Supporting Information E, Table S3). Unexplained residual covariance was, on average, |4.5%| of the covariance (for synergies 5.5% and for trade-offs -3.6%), suggesting a low amount of random covariation between EFs.

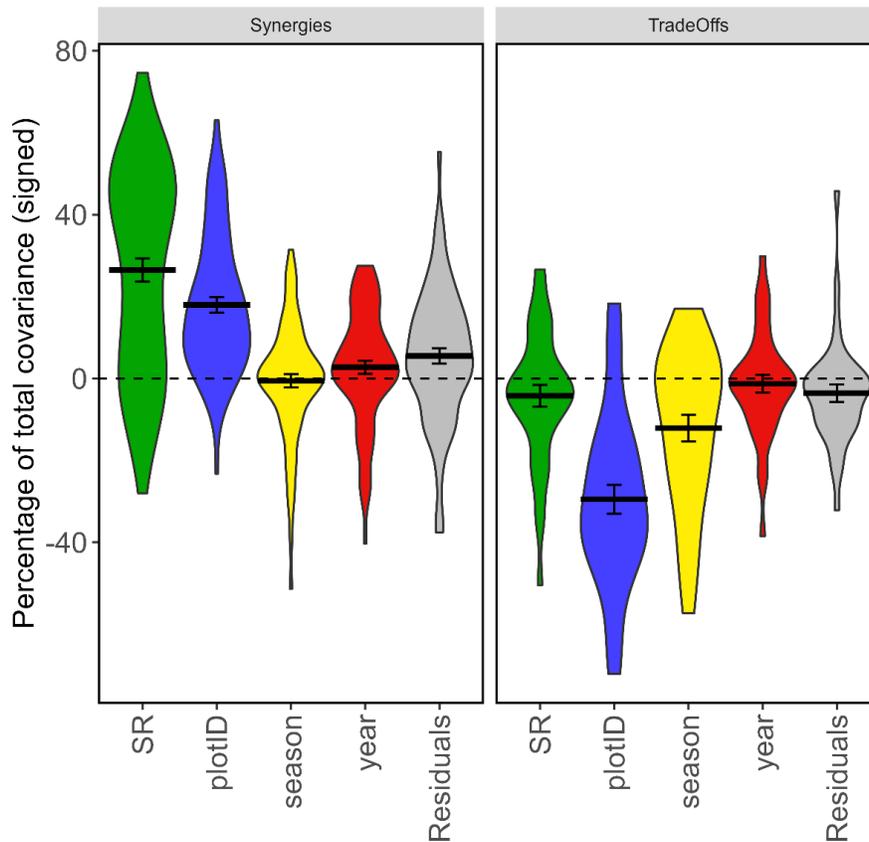


Figure 3: The contribution of SR, plot ID, season and year to total covariance between the 116 pairs of EFs, separated for EF pairs showing positive relationships (synergies, 78 pairs) and negative relationships (trade-offs, 38 EF pairs) according to their mean correlation. The violin plots show for each driver the mean (solid line), the standard error, and the distribution of contributions to covariance of EF pairs. Positive contributions indicate that the driver causes positive covariances between pairs of EFs, synergistically driving

the two individual EFs. Negative contributions indicate that the driver causes negative covariances between pairs of EFs, driving the two individual EFs antagonistically. Results are derived by partitioning overall covariances into contributions of the different drivers; see method section for explanation. In this graph, only effects are shown, which on average explain >5% of covariance. In Supporting information F), the same graph with all variables (including FGR, and the presence/ absence of grasses, legumes and herbs) is shown.

DISCUSSION

We investigated the variation in the correlations between different EFs and the drivers of these relationships. We found that correlations were variable, and correlations between two particular EFs could range from weak to strong or from negative to positive among the repeated measurements. Overall, EF pairs generally showed an increasing variation in their correlations with a higher number of times the EF-pair was measured. The correlations among pairwise EFs were differently affected by the identity of time points (years and seasons). That means that some EF-pairs showed more stable correlations throughout time, whereas other EF-pairs were more affected by differences in years and seasons and therefore showed a higher temporal variation. Species richness and plot identity (including the presence of legumes, grasses, herbs) explained the largest fraction of covariance among EFs, while the effects of time (year, season, and their interaction) explained little covariance. We found that most of the covariance for synergies was explained by species richness (~26.5%), whereas for trade-offs, most covariance was explained by plot identity (-29.5%). Time explained 13.4% of covariance for trade-offs but little for synergies (3.3%). Correlations among EFs and the drivers of these correlations varied over time. These results indicate the importance of repeated measurements of ecosystem functions (EFs) over time to avoid spurious conclusions, and suggests that land management practices that promote biodiversity and reduce negative identity effects can enhance multifunctionality in grasslands.

We found that even under the controlled conditions of our experiment, correlations among EFs were variable. High temporal variation of individual EFs had been documented before (Carpenter, Mooney et al. 2009, Cardinale, Duffy et al. 2012, Gaglio, Aschonitis et al. 2020, Qiu, Carpenter et al. 2020, van der Plas, Schröder-Georgi et al. 2020). However, until now, inconsistent correlations between EFs or classes of EFs have only been found when different studies were compared (Lee and Lautenbach 2016). Although all functions were measured with a consistent methodology at a single field site. Trade-offs were as variable as synergies (Supporting information E, Fig. S5), and relationships for many pairs of functions could range from synergy to trade-off when correlations were calculated for different time points, which confirms the previous study of Lee and Lautenbach (2016). Lee and Lautenbach (2016) found that the agreement on the type of relationship for a particular pair of EFs, i.e. synergy, trade-off, or no-effect relationship, decreased the more often the relationships were measured. Similarly, we found that the variability of EF relationships increased with the number of measurements (Supplementary information E, Fig. S6), which indicates, that single measurements can be misleading when EF relationships are identified. Furthermore we showed, that not the identity of time points (years and seasons), but the identity of EF pairs were associated with a high variation in EF relationships (Supporting information, Fig S7). That means, that it depends on the particular EF pair, whether their correlation was highly variable because of differences between years or seasons. One explanation could be that ecosystem processes vary caused by a change or adjustment of biotic assemblages as a response to their environmental conditions (Turner and Chapin 2005), leading to changes in EF relationships or multifunctionality with changing environmental conditions (Zirbel, Grman et al. 2019). In our study, the variation in relationships between EFs originated from the temporal variation in EF drivers (possible reasons could be inter-annual variation in rainfall, temperature or other cyclic patterns such as boom and bust cycles of herbivory), while in Lee and Lautenbach (2016), the variation in the relationships among classes of EFs was introduced by different studies, and therefore additional site-dependent contexts.

Regarding the identified EF relationships (mean correlations among all the different EFs), we found both, synergies and trade-offs that can be explained by biological processes and therefore confirm other studies investigating the individual EFs (Jarrell and Beverly 1981, Allan, Weisser et al. 2013). For example, EFs

of the classes plant nutrients and plant productivity showed often a trade-off, indicating a dilution effect. i.e. when plant growth improved, plant nutrient concentrations decreased in the plant tissue (Jarrell and Beverly 1981). However, the carbon concentration of plants (PlantC) showed mainly synergies with EFs of the class plant productivity. One reason could be that a high biomass reflects a high nutrient-efficiency and thus comparatively low nutrient concentrations and correspondingly high C concentrations (Allan, Weisser et al. 2013). Furthermore, organic carbon in the soil (SoilDOC, SoilCorg) was positively related to plant productivity (Fig. 2). This is consistent with studies, showing that a high biomass production leads to an accumulation of dead plant material in the soil (Post and Kwon 2000) or root exodation of plants (Raich and Tufekciogul 2000). As the Jena experiment was established on depleted arable soil, a higher carbon concentration in the soil occurred faster with higher biomass production, but in the end the carbon concentration might be the same on all plots due to accelerated litter decomposition (Weisser, Roscher et al. 2017). EFs of the class Invasion resistance showed synergies with EFs of the class plant productivity. This is consistent with former studies, showing that a high biomass of the native species suppressed invasive species (Yannelli, MacLaren et al. 2020, Rojas-Botero, Kollmann et al. 2022), often due to a more complete use of available resources (Hector, Dobson et al. 2001, Roscher, Beßler et al. 2009). Summarizing these examples, the relationships identified here for the classes of EFs are consistent with the underlying biological processes.

We found that synergies and trade-offs have different drivers. Species richness is a known driver of many EFs (Gamfeldt and Roger 2017, Weisser, Roscher et al. 2017, Craven, Eisenhauer et al. 2018) and ecosystem services (van der Plas 2019). When two EFs improve with higher SR, a positive covariance is introduced, strengthening their relationship. The fact that we showed that SR affected the majority of investigated EFs positively explains that the large majority of SR effects on the covariance between EFs were positive and that EFs in synergies were stronger effected by SR than EFs in trade-offs (Fig. 2). However, the relationship between two EFs weakens when SR has contrasting effects on the two EFs, as indicated by a few pairs of EFs for which we showed SR to cause negative covariance. In our study, plot identity represents all other differences among plant communities within a diversity level, such as FGR, the presence of different functional groups (Supporting information F, Fig S8), species identity, and the presence of other groups of organisms (e.g. microbes, insects) associated with particular plant communities. These identity effects were mostly positive for EFs in synergies and mostly negative for EFs in trade-offs. This can be explained by selection effects, which have been documented repeatedly by comparing the performance, such as biomass production, of plant communities (Marquard, Weigelt et al. 2009). A high performance of a plant community may be associated with a high abundance of certain species (Loreau and Hector 2001) and therefore with many simultaneously occurring EFs (many synergies). A low performance is associated with a negative selection effect (Loreau and Hector 2001) and could be related to the occurrence of just a few EFs, as they are restricted by trade-offs. Outside an experimental setup, the equivalent of SR and plotID would be the different communities associated with landscape patches. As a consequence of different biotic communities, different levels of individual EFs would occur in these patches and different correlations among EFs could be identified. While the effect of different aspects of SR and plotID (FGR, presence/absence of functional groups or individual species) on individual EFs is frequently investigated, further research is needed to identify how different SR/ plotID impacts the relationships between EF.

Time (year, season, and their interaction) explained some, albeit little, covariance among EFs and affected synergies and trade-offs differently. Time can become a driver of EF relationships when environmental conditions vary over time, e.g., temperature and extreme events, affecting the biological activity of organisms. Trade-offs were more affected by temporal effects than synergies. Season was among the main drivers of trade-offs, reflecting the pronounced change in abiotic conditions among seasons in the temperate zone. As an example, soil microbial activity strongly responds to climatic conditions, affecting carbon and nutrient cycling (Frey, Lee et al. 2013). Further, competition strongly affects trade-offs, which can be changed by altering the environmental conditions, such as the availability of water or light that fluctuate with time. Consequently, temporal variability in these drivers can induce variability in EF correlations underlying the importance of repeated measurements to identify the true relationships between EF.

When investigating the drivers of EF correlations, we found that some covariance among EFs could not be

explained by any of the drivers tested in our study. We interpret this unexplained covariance as EF pairs affected by the ecological-constraints-mechanism. Plants have access to a limited pool of resources they can invest in, e.g. in growth or defence against natural enemies, resulting in a growth-defence trade-off (Karasov, Chae et al. 2017). Because providing unlimited resources within a local patch is impossible, ecological trade-offs resulting from resource limitation are inevitable. Further, the simultaneous provision of EFs can be limited by competition. For example, in our study, improved plant productivity was associated with higher invasion resistance (considered good), likely due to intensified competition for space and light between the resident plant community and potential invading plant individuals in our plots. Furthermore, the higher the root biomass was, the lower were the soil nutrient concentrations, implying competition among plant species for available nutrients. Resource limitations and competition may limit biological activities, leading to trade-offs between EFs. These trade-offs can be weakened when competition in diverse communities is reduced by complementarity between species (Weisser, Roscher et al. 2017). Understanding how ecological constraints affect relationships between EFs is an important topic for further investigation.

Our results have implications for land management aiming at promoting multifunctionality. Relationships among EFs affect multifunctionality since they can either promote (synergies) or limit (trade-offs) multifunctionality. Analysing the drivers of relationships between EFs, we showed that SR can promote synergies among EFs, resulting in increased multifunctionality. Consequently, promoting diversity is a mean to foster multifunctionality, confirming previous empirical biodiversity multifunctionality relationships (Isbell, Calcagno et al. 2011, Lefcheck, Byrnes et al. 2015, Meyer, Ptacnik et al. 2018). Further, we showed that plot identity effects, including functional group richness and the presence/absence of individual functional groups, were important drivers for trade-offs between EFs. While we tested for identity effects of plots, there are likely individual plant species that cause these trade-offs by maximising some EFs at the expense of other EFs. When future research can identify such plant species with strong effects on trade-offs, land management can target low densities of these disadvantageous species to reduce trade-offs between EF and promote multifunctionality. Nevertheless, competition for resources and the resulting ecological trade-offs between EFs are challenging to resolve.

CONCLUSIONS

Our study showed that even under the controlled conditions of a single experimental field site, correlations among EFs were variable over time. Consequently, repeated measurements of EF are needed to avoid spurious and non-generalisable conclusions about relationships among EFs.

Moreover, our results show the potential for land management to promote multifunctionality in both the establishment and the management phase by incorporating two principles. First, maintaining or increasing biodiversity of grasslands, which we showed increases synergies among EFs, promoting multifunctionality. Second, reducing negative identity effects by reducing the proportion of disadvantageous species or communities as indicated by the strong effect of plot identity strengthening trade-offs.

Future studies should continue to investigate the drivers of EF relationships to identify common drivers causing trade-offs and separate common drivers from potential ecological constraints. Importantly, these studies should also address how environmental conditions can change these relationships and identify influential species enabling recommendations on how to adapt management for maximising multifunctionality.

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