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Dominance vs. complementarity: A global analysis of the influence of plant functional community structure on ecosystem functioning measured as NDVI

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One diversity that matters is that of the people studying it.

Acknowledgements

1 Resumo

2 Diversos estudos teóricos, experimentais e observacionais têm demonstrado que as relações

3 entre a biodiversidade e as funções ecossistêmicas (BEF) são determinadas pela estrutura

4 funcional da comunidade (ou seja, pela distribuição dos atributos das suas espécies

5 constituintes). Isso pode ocorrer por meio de dois mecanismos mutuamente não exclusivos: (1)

6 a hipótese de dominância (também denominada de efeito de relação de massa), na qual os

7 processos ecossistêmicos são influenciados pela média ponderada na comunidade de um dado

8 atributo funcional (CWM) considerado relevante; (2) a hipótese de complementaridade, na qual

9 a maior variabilidade de um atributo funcional na comunidade (FD) é uma expressão da

10 complementariedade de nicho, o que beneficia o desempenho dos processos ecossistêmicos.

11 Embora ambos os mecanismos já tenham sido amplamente estudados em comunidades de

12 plantas em pequenas escalas espaciais, análises globais considerando distintos biomas ainda são

13 necessárias. Neste estudo, a relação entre biodiversidade e funcionamento dos ecossistemas foi

14 avaliada com base na integração entre uma base de dados global de parcelas de vegetação

15 (sPlot), uma base de dados de atributos de espécies de plantas (TRY) e dados do Índice de

16 Vegetação por Diferença Normalizada (NDVI) obtidos por sensoriamento remoto. O objetivo foi

17 verificar, simultaneamente, os efeitos de dominância e de complementaridade sobre a

18 produção de biomassa vegetal em ecossistemas campestres em todo o mundo. Os dados sobre

19 a estrutura funcional das comunidades (CWM e FD) foram obtidos a partir da base de dados

20 sPLOT e TRY, utilizando para isso 18 atributos funcionais de plantas ecologicamente relevantes.

21 O NDVI, considerado como aproximação da produtividade da vegetação, representa uma

22 medida do funcionamento do ecossistema e foi obtido a partir do produto MOD13Q do sensor

23 MODIS, com resolução espacial de 250m. Para garantir que as medidas de NDVI fossem

24 derivadas apenas de ecossistemas campestres, sem a interferência de outras fisionomias

25 vegetais, foram descartadas as parcelas do sPlot com presença de paisagens heterogêneas no

26 seu entorno mediante consulta a um mapa global de cobertura e uso da terra (Globcover2009).

27 Para quantificar os efeitos independentes da dominância e da complementaridade sobre as

28 variações no NDVI , com controle das variáveis climáticas, foi utilizada uma análise de regressão

29 múltipla do tipo *commonality*. Os resultados demonstraram que o principal preditor da variação

30 no NDVI correspondeu a um conjunto de atributos funcionais das espécies dominantes

31 relacionados com o espectro de economia da comunidade vegetal (atributos *fast-slow*),

32 indicando a prevalência da hipótese de dominância (R^2 ajustado = 0,65). Os efeitos evidentes

33 da dominância e os efeitos potenciais da complementariedade são discutidos no contexto da

34 sua relação com os fatores abióticos, sendo que a precipitação pluviométrica, em particular,

35 parece ter maior influência tanto sobre a composição de atributos quanto sobre a
36 produtividade. Apesar de algumas limitações metodológicas, a abordagem inovadora utilizada
37 neste trabalho pode ajudar a esclarecer as relações entre biodiversidade e funções
38 ecossistêmicas em escala global, dentro de uma perspectiva integradora e baseada em dados.

39 **Palavras-chave:** *atributos funcionais, ecologia funcional, biodiversidade e funções*
40 *ecossistêmicas, sensoriamento remoto, sPlot, vegetação campestre, ecologia global.*

Abstract

Theoretical, experimental and observational studies show that biodiversity ecosystem functioning (BEF) relationships are determined by functional community structure (i.e. trait distributions in a community) through two mutually non-exclusive mechanisms: (1) The *dominance hypothesis* (a.k.a. mass ratio effect) links ecosystem processes to the community weighted mean (CWM) of a relevant effect trait. (2) The *complementarity hypothesis* states that higher variability of a trait value within a community (FD) reflects niche complementarity enhancing ecosystem processes. While both mechanisms have been extensively studied in plant communities at small spatial scales, there is a need for global analyses across biomes. Here, a data driven approach to the BEF question is presented integrating a global vegetation plot database with a trait database and remotely sensed NDVI. The objective of this study was to simultaneously evaluate dominance and complementarity effects in grassland systems worldwide. Data on functional community structure (CWM and FD) were obtained from the global vegetation plot database sPlot in combination with the plant trait database TRY using 18 ecologically relevant plant traits. Ecosystem functioning at the selected sPlot sites (n = 2941) was measured as NDVI at a spatial resolution of 250m using the MODIS product MOD13Q (annual peak NDVI being a proxy of productivity). The landcover map Globcover2009 was used for characterization of landscape heterogeneity and landcover at each site, and plots in heterogeneous non-grassland pixels were discarded. Multiple regression commonality analysis was used to disentangle the contributions of complementarity and dominance effects to the variation in NDVI, while controlling for climate variables (adjusted R^2 = 0.65). The results show that a *plant community economics spectrum* referring to the "fast-slow traits" of the dominant species in the community was the strongest predictor of the NDVI values in the grassland systems (dominance effect). Both, evident dominance and potential complementarity effects are discussed against the background of their interplay with abiotic factors and it is noted that especially precipitation seems to drive trait composition and productivity. Despite methodological shortcomings, the novel approach presented in this paper is considered a step towards a more integrative data-driven BEF debate at the global scale.

Keywords: *plant functional ecology, biodiversity ecosystem functioning, remote sensing, sPlot, grasslands, global ecology, plant community economics spectrum.*

Zusammenfassung

Theoretische, experimentelle und beobachtende Studien zeigen, dass Beziehungen zwischen Biodiversität und Ökosystemfunktionen (BEF) von funktioneller Gemeinschaftsstruktur bestimmt sind und dass dabei zwei sich gegenseitig nicht ausschließende Mechanismen eine Rolle spielen: (1) Die *Dominanzhypothese* (Massenverhältniseffekt) stellt einen Zusammenhang zwischen den durch Artenabundanz gewichteten Mittelwert von Effektmerkmalen in der Gemeinschaft (CWM) und Ökosystemprozessen her. (2) Die *Nischen-Komplementarität-Hypothese* beschreibt, dass eine höhere Variabilität eines Merkmals innerhalb einer Gemeinschaft (FD) komplementäre Nischen widerspiegelt, die zu einer effizienteren Ressourcennutzung führen and dadurch Ökosystemprozesse verbessern. Während beide Mechanismen in Pflanzengemeinschaften auf kleinen räumlichen Skalen umfassend untersucht wurden, besteht ein Bedarf an globalen Analysen über Biomgrenzen hinweg. Hier wird ein datengetriebener Ansatz für die BEF-Frage vorgestellt, der eine globale Vegetationsdatenbank mit einer Datenbank für Pflanzenmerkmale und Fernerkundung integriert. Ziel dieser Studie war es, Dominanz- und Komplementaritätseffekte in Grünlandsystemen weltweit zu bewerten. Die Daten zur funktionellen Gemeinschaftsstruktur (CWM und FD) wurden aus der globalen Vegetationsdatenbank sPlot in Kombination mit der Merkmaldatenbank TRY mit 18 ökologisch relevanten Pflanzenmerkmalen gewonnen. Ökosystemfunktionen wurden an den ausgewählten sPlot-Standorten (n = 2941) bei einer räumlichen Körnung von 250 m als jährliches NDVI maximum mit dem MODIS-Produkt MOD13Q gemessen, das als Proxy für Produktivität gilt. Es wurde eine Kommunalitätsegressionsanalyse verwendet, um die Wirkungen von Dominanz- und Komplementaritätseffekten auf die Variation des NDVI bei Berücksichtigung von Klimafaktoren zu entwinden (adjusted R^2 = 0.65). Die Ergebnisse zeigen, dass ein *plant community economics spectrum*, das die "schnell-langsam-Merkmale" der dominanten Arten in der Gemeinschaft beschreibt, der stärkste Prädiktor für die NDVI-Werte in den Grünland-Systemen war (Dominanz-Effekt). Sowohl offensichtliche Dominanz- als auch potenzielle Komplementaritätseffekte werden vor dem Hintergrund ihres Zusammenspiels mit abiotischen Faktoren diskutiert und es wird gezeigt, dass vor allem Niederschlag die Merkmalsverteilung und Produktivität zu bestimmen scheint. Trotz methodischer Mängel wird der neuartige Ansatz, der in hier vorgestellt wird, als ein Schritt zu einer integrativeren datengesteuerten BEF-Debatte auf globaler Ebene betrachtet.

Schlüsselwörter: *Funktionelle Pflanzenökologie, Ökosystemfunktionen, Fernerkundung, sPlot, Grünland, globale Ökologie, plant community economics spectrum.*

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Introduction

The question of how biodiversity influences ecosystem functions, such as biomass production and biogeochemical cycling, has been a widely discussed topic for decades (Hooper *et al.* 2005), often referred to as the biodiversity ecosystem functioning (BEF) debate. In the face of an ongoing global biodiversity crisis (Ceballos *et al.* 2015; McGill *et al.* 2015), researchers have been trying to understand how changes in diversity and composition of biological communities (especially primary producers) affect ecosystem processes and services, and have provided strong evidence that productivity tends to increase with species richness (Cardinale *et al.* 2011). To understand the mechanistic basis of this relationship the focus of BEF research has moved on to investigating how functional characteristics of species in a system rather than species richness per se drive ecosystem processes (Díaz & Cabido 2001; Cadotte, Carscadden & Mirotchnick 2011; Cadotte, Albert & Walker 2013; Dias *et al.* 2013; Lavorel 2013; Ebeling *et al.* 2014). Species traits have been recognised as the key to understanding both, the responses of species to environmental factors (response traits) and the effect they have on ecosystem processes (effect traits) (Lavorel & Garnier 2002). Trait-based approaches have offered two main hypotheses for a mechanistic explanation of how functional community structure (i.e. the distribution of trait values measured in a given community; Garnier, Navas & Grigulis 2016) influences ecosystem functioning: The dominance hypothesis (also "mass ratio hypothesis") states that ecosystem processes are primarily determined by effect traits of the dominant species in a community (Grime 1998) which emphasizes the importance of the abundance weighted mean of the species' effect traits (Garnier 2004). The complementarity hypothesis, in contrast, refers to the variation of a trait value within a community. It suggests that a higher range of trait values (i.e. functional diversity) reflects niche complementarity allowing for enhanced resource use and ecosystem functioning (Petchey & Gaston 2006). As these hypotheses are not mutually exclusive, their suggested mechanisms may act simultaneously. Both, experimental and observational studies on biomass production in plant communities tend to find dominance effects more frequently and with stronger evidence, than complementarity effects (Mokany, Ash & Roxburgh 2008; Mouillot *et al.* 2011; Lavorel 2013; Chollet *et al.* 2014). Especially, plant traits related to the trade-off between resource acquisition and conservation, which is known as the "leaf economics spectrum" (Wright *et al.* 2004), show strong links to productivity caused by the trait values of the most dominant species in the community (Diaz *et al.* 2004; Grigulis *et al.* 2013; Lavorel 2013). Recent studies, however, show that the combined contributions of both, functional diversity and mass ratio effects, are responsible for the simultaneous provisioning of multiple ecosystem functions and services, referred to as multifunctionality (Hector & Bagchi

180 2007; Mouillot *et al.* 2011; Valencia *et al.* 2015) as well as for biomass production outside of the
181 high productivity season (Chollet *et al.* 2014).

182 Methodological challenges to the clear separation of dominance and complementarity effects
183 have been posed by a lack of independence between functional diversity metrics and
184 community-weighted mean trait values (Ricotta & Moretti 2011) as well as by the many
185 confounding factors and environmental covariates influencing ecosystem processes (Díaz *et al.*
186 2007). These problems were addressed through the design of appropriate experimental layouts
187 with controlled conditions (Dias *et al.* 2013; Eisenhauer *et al.* 2016) and adequate statistical
188 methods in natural systems (Grace *et al.* 2007; Mokany, Ash & Roxburgh 2008). While traditional
189 approaches have tried to keep abiotic factors constant, restricting themselves to small spatial
190 and temporal scales, more recent approaches have specifically included or manipulated
191 environmental variation such as climate and nutrient supply (Schumacher & Roscher 2009;
192 Roscher *et al.* 2013; Chollet *et al.* 2014; Zhou *et al.* 2017).

193 Regardless of these advances, there continues to be a lack of studies on large spatial scales
194 across biomes (but see Cornwell *et al.* 2008; Musavi *et al.* 2015), and despite its vital role for
195 ecosystem processes, plant functional community structure has only very poorly been
196 implemented in earth system models (but see Van Bodegom, Douma & Verheijen 2014). While
197 a global coordination and upscaling of the measurement of plant functional community
198 structure and ecosystem process are logistically challenging using traditional approaches,
199 modern ecology has entered the era of "big data" which offers powerful alternatives (Hampton
200 *et al.* 2013): global initiatives compile community data and species characteristics into large
201 databases (Kattge *et al.* 2011), and new ecosystem observation techniques like remote sensing
202 and flux measurements offer novel approaches to the quantification of ecosystem processes
203 (Baldocchi *et al.* 2001; Ustin *et al.* 2004; Houborg, Fisher & Skidmore 2015). In a conceptual
204 paper on large scale BEF research, Musavi *et al.* (2015) present a data driven approach linking
205 trait information to so called ecosystem functional properties (EFP) derived from eddy
206 covariance (Reichstein *et al.* 2014). While their approach is highly quantitative and scalable from
207 the leaf to the ecosystem level, there is still a mismatch between sites covered by flux
208 measurements and available trait information (Musavi *et al.* 2017).

209 Here, we present an approach using the world's largest repository of plant community data sPlot
210 coupled with the plant trait database TRY (Kattge *et al.* 2011) and the globally available
211 normalized difference vegetation Index (NDVI) to tackle the biodiversity ecosystem functioning
212 question at the planetary scale. The combination of NDVI and trait databases has been used

213 before to study the diversity-resilience relationship at a regional scale (Spasojevic *et al.* 2016).
214 Taking advantage of over a decade worth of vegetation surveys from around the globe, the
215 combination of a global vegetation plot database with trait data and satellite retrievals is a novel
216 approach to address diversity-productivity relationships at the global scale. In line with a long
217 tradition of BEF research in grassland ecosystems (Tilman, Wedin & Knops 1996; Hector *et al.*
218 1999; Hooper *et al.* 2005; Wu *et al.* 2015), grasslands were chosen as a model system for this
219 analysis although the methodology could also be applied to other vegetation types. The specific
220 objective of this study was to investigate the effect of plant functional community structure on
221 NDVI in grasslands around the world. In accordance with the overwhelming evidence in the
222 literature, it was hypothesised that dominance effects would be stronger than complementarity
223 effects.

224 # Material and methods

225 ## Datasets

226 Being purely data driven, this study was based on the integration of data compiled from three
227 global initiatives: (1) the global vegetation plot database sPlot (version 2.1) which provides
228 georeferenced surveys of plant communities all over the world (see:
229 https://www.idiv.de/?id=176&L=0), (2) the TRY database of species functional traits (Kattge et
230 al. 2011) and (3) the MODIS product MOD13Q1 (Didan 2015) providing the vegetation index
231 NDVI which was used as a proxy for ecosystem level primary productivity. The sPlot database
232 contains information on plant community composition in over 1.1 million vegetation plots
233 contributed by more than 100 vegetation plot databases. Here, sPlot was sampled to
234 characterise functional structure in grassland communities around the globe by integrating the
235 vegetation plot data with species trait data from TRY.

236 At every location selected from sPlot, the satellite derived Normalized Difference Vegetation
237 Index (NDVI) was calculated as the ratio between the difference and sum of near infrared and
238 red surface reflectance. NDVI is a measure of surface greenness, closely related to vegetation
239 dynamics (Rouse *et al.* 1974). Considered a proxy of primary productivity (Running 1990; Paruelo
240 *et al.* 1997) and other ecosystem processes (Ustin *et al.* 2004), NDVI has been used in ecological
241 studies to evaluate ecosystem responses to environmental changes (reviewed in Pettorelli et al.,
242 2005) and to derive ecosystem stability metrics (De Keersmaecker *et al.* 2014). The NDVI dataset
243 used here was the MODIS product MOD13Q1, which has global coverage with a pixel size of 250
244 m and a temporal resolution of 16 days.

245   Integrating vegetation plot data with remotely sensed NDVI comes along with scale issues as a

246   MODIS pixel is 2 orders of magnitude larger than a typical vegetation plot. This scale

247   incompatibility becomes problematic in cases where a plot is located within a NDVI pixel that is

248   very heterogeneous with other cover types different from grassland (mixed pixel).

249   Consequently, sPlot community data at the plot level might not appropriately represent the

250   overall plant community at the scale of the NDVI pixel. To overcome this problem, the land cover

251   map GlobCover 2009 (Arino *et al.* 2010) was used to identify and exclude vegetation plots that

252   were located in NDVI pixels contaminated with non-grassland land uses (e.g. forest, agricultural

253   land, urban areas).

254   Further, for every plot location included in this study, mean annual temperature and annual

255   precipitation values were retrieved from the CHELSA project which provides bioclimatic

256   variables at a global scale at a resolution 30 arc sec (Karger *et al.* 2016). As climate is a major

257   driver of biomass production and vegetation dynamics in grassland systems (Sala *et al.* 1988;

258   Briggs & Knapp 1995; La Pierre *et al.* 2011; Chollet *et al.* 2014), these variables were included as

259   covariates in the analysis.

260   Sampling of sPlot

261   sPlot was screened for observations from grassland communities. Any selected plot had to

262   satisfy at least one of the following criteria: (1) The plot was marked as "grassland" by the

263   vegetation survey that provided the sPlot entry. (2) At least 90 % of the plot was covered by

264   species that were not trees or shrubs or that were shorter than 2 m in plant height (according

265   to the TRY database). Furthermore, at least 50% of the relative vegetation cover in a plot had to

266   consist of plant species represented in TRY. Excluded were plots that were labelled as "forest",

267   "shrubland" or "wetland", as well as observations prior to the year 2000 (launch of the MODIS

268   program). Further, excluded were plots with high location uncertainty (> 100m) and unprecise

269   GPS coordinates (< 4 decimal places in decimal degrees). To filter out mixed NDVI pixels, all

270   selected plots had to be located within a MODIS pixel whose land cover consisted to at least 95

271   % of the GlobCover 2009 categories "mosaic grassland", "closed to open herbaceous

272   vegetation" and "sparse vegetation" in any relative composition, which was assumed to

273   correspond to grasslands.

274   NDVI time series

275   Complete NDVI time series (MOD13Q1) were retrieved by using Google Earth engine (Google

276   Earth Engine Team 2015) for each of the selected vegetation plots. From each time series, the

277   maximum annual NDVI values were extracted for the year of the respective vegetation survey

278 as well as the respective following year. This peak NDVI value corresponds to yearly maximum

279 photosynthetic activity of the vegetation and is an indicator for overall productivity and biomass

280 (Pettorelli *et al.* 2005). The mean of the two annual maximum values was considered the NDVI

281 response variable for a given plot. The consideration behind this approach was that averaging

282 across two subsequent years is likely to reduce the effect of anomalies and noise in the NDVI

283 measured by remote sensing, leading to more robust NDVI values. In cases where a NDVI pixel

284 contained more than one vegetation plot, surveys from different years were treated as

285 independent observations. For vegetation plots that were described in the same year in the

286 same NDVI pixel, just one plot was drawn at random.

Plant traits and their ecological importance

288 Eighteen ecologically relevant plant traits were used to characterise the functional community

289 structure at all selected plots. Species mean traits were retrieved from TRY (Kattge et al. 2011)

290 and gap-filled using Bayesian Hierarchical Probabilistic Matrix Factorization (Schrodt et al. 2015).

291 All trait values were log transformed. A detailed description of the gap filling procedure and

292 matching between sPlot and TRY will be given by Bruelheide et al. *(in press.)*, who provided these

293 data for the sPlot initiative and this study. The gap-filled trait data were available for 88.7% of

294 all species occurrences in sPlot.

295 The traits included represent different ecological trade-offs and plant strategies: Specific leaf

296 area (i.e. the one-sided leaf area divided by leaf mass), Leaf N, Leaf P, Leaf C per dry Mass, Leaf

297 N per area and Leaf dry matter content are traits related to leaf-level carbon gain strategies or

298 the so called "leaf economic spectrum" LES (Wright *et al.* 2004). The LES spans a trait axis ranging

299 from "conservative" species with long-lived, physically robust leaves with low photosynthetic

300 rate and poor litter quality to "acquisitive" species with short-lived leaves that exhibit high C

301 assimilation rates and have a higher nutritive value (Chapin 1980; Reich, Walters & Ellsworth

302 1997; Wilson, Thompson & Hodgson 1999; Wright *et al.* 2004; Garnier, Navas & Grigulis 2016).

303 The LES is known to be a strong driver of ecosystem processes such as productivity and litter

304 decomposition, with higher rates found in communities dominated by "acquisitive" species (Diaz

305 *et al.* 2004; Grigulis *et al.* 2013; Lavorel 2013). The traits seed number of the reproductive unit,

306 dispersal unit length, seed length and seed mass reflect a reproductive trade-off between seed

307 competitive ability and survival on the one hand and dispersal rate and colonization on the other

308 hand (Smith & Fretwell 1974; Moles & Westoby 2006). Although seed traits are not expected to

309 have a strong direct influence on ecosystem productivity, they tend to covary with plant size and

310 other life history traits that might have a stronger link with ecosystem processes (Thompson &

311 Rabinowitz 1989; Rees & Venable 2007; Moles & Leishman 2008). The trait plant height is linked

to competitive ability of individual plants and light interception (Gaudet & Keddy 1988; Violle *et al.* 2009), hence it reflects carbon acquisition strategies at the individual level (King 1990; Westoby *et al.* 2002). Being an indicator of overall plant size, plant height is an important component of standing biomass in the community (Chave *et al.* 2005). Also, the trait leaf area is allometrically connected to plant stature and plant height (Niklas 1994; Ackerly & Donoghue 1998). Furthermore, leaf area plays a crucial role in light interception and influences leaf energy and water balances as well as temperature (Farquhar, Buckley & Miller 2002). Both, leaf area and leaf fresh mass contribute to the LES via their ratio, specific leaf area. The trait stem density represents a trade-off between rapid growth and high turnover on one hand and slow growth, higher structural stability and survival on the other hand, which is conceptually similar to the LES (Chave *et al.* 2009; Freschet *et al.* 2010; Wright *et al.* 2010). Stem characteristics such as the traits wood vessel length and stem conduit density are also strong drivers of plant hydrology and thus influence evapotranspiration at the ecosystem level (Zanne *et al.* 2010). Although the latter are more commonly used for woody species (Chave *et al.* 2009), they have also been included in this study on grasslands to achieve a more holistic characterisation of the functional community structure that goes beyond the commonly measured leaf traits for herbal vegetation. The traits leaf N to P ratio and Leaf nitrogen isotope ratio (Leaf delta ^{15}N) are connected to plant nutrient supply and status. N to P ratios give an indication of nutrient limitations in the system and exhibit a correlation with biomass production (Güsewell 2004). Leaf nitrogen isotope ratios are linked to different nitrogen sources and might give an idea of the relative importance of mycorrhizae and nodule derived nitrogen in the communities (Craine *et al.* 2015).

Functional community structure

Community weighted mean (CWM) and Rao's quadratic entropy (Q) were chosen to characterise the functional community structure in every plot based on the 18 traits discussed above. CWM is an abundance weighted trait mean value of the community that represents the trait values of the most dominant species and is therefore linked to the mass ratio effect and dominance hypothesis (Garnier 2004). Rao's quadratic entropy is a generalisation of the Simpson's index (Rao 1982) that has been used to quantify functional diversity of communities using functional dissimilarity matrixes calculated for single or multiple species traits (Botta-Dukat 2005; Lepš *et al.* 2006). Together, Rao's quadratic entropy and CWM have been applied in biodiversity ecosystem functioning research to disentangle dominance and complementarity effects as indicated by "mean" (i.e. CWM) and "dispersion" (i.e. Q) of traits, respectively (Ricotta & Moretti 2011). Here, single trait CWM and Q were calculated as follows:

Eq. 1

$$CWM_{l,k} = \sum_{i=1}^{n_k} p_{i,k} t_{i,l}$$

346   where n_k is the number of species in plot k, $p_{i,k}$ is the relative cover of species i in plot k, and $t_{i,l}$

347   is the mean value of species i for trait l.

Eq. 2

$$Q_{l,k} = \sum_{i=1}^{n_k} \sum_{j=1}^{n_k} d_{i,j,l} p_{i,k} p_{j,k}$$

348   where n_k is the number of species in plot k, $p_{i,k}$ and $p_{j,k}$ are the relative covers of species i and j

349   in plot k, and $d_{i,j,l}$ is the dissimilarity, in the range of 0–1, between species i and j based on trait

350   l. The dissimilarity metric used was Gower's distance (Podani 1999) and the computation of Q

351   was performed in the R package SYNCSA (Debastiani & Pillar 2012).

352   To reduce the functional trait space described by the 18 CWM variables, a principal component

353   analysis (PCA) was performed on the CWM values in all selected communities (correlation-based

354   using the R package FactoMineR). The PCA axes were considered as latent variables summarizing

355   most of the variation in CWM across multiple traits. These latent variables are integrated

356   measures characterising the dominant species in a community and are therefore linked to the

357   dominance hypothesis (Chollet *et al.* 2014). The first two axes of variation (PCA.1 and PCA.2)

358   were included in the multiple regression model for the NDVI response.

359   Rao's quadratic entropy was recalculated across multiple traits by averaging the single trait $Q_{l,k}$

360   values, which was possible because the distance matrix was standardised in the range of 0 to 1,

361   respectively . This was done for all $18^2 - 1$ possible combinations of the 18 traits, and for each

362   combination a simple regression was performed using the corresponding Q as predictor of NDVI.

363   The trait combination with the strongest effect size on NDVI was selected as the predictor

364   variable for functional diversity, *FD* (Mokany, Ash & Roxburgh 2008). This was the case for the

365   trait combination stem conduit density and stem density.

366   Data analysis

367   Multiple linear regression analysis was used to explore the role of biotic and abiotic factors on

368   the response variable NDVI. The multiple regression model was specified in R using the function

369   "lmp()" from the package "lmPerm" that allows permutation test for linear models (Wheeler &

370   Torchiano 2016). This approach was adopted because of non-normality in the NDVI data. Next

371   to the variables of functional community structure (PCA.1, PCA.2, FD), the covariates annual

372   mean temperature (Temp), annual precipitation (Prec) and absolute latitude (Lat) of the plot

373   were included in the model. The latter three variables were centred and standardized before

374   entering the model. The absolute value of the latitude was selected to achieve a more linear

375   relationship with NDVI. The model was defined as follows:

376   $$NDVI \sim PCA.1 + PCA.2 + FD + Prec + Temp + Lat$$

377   Instead of using stepwise or hierarchical regression approaches that - among other

378   shortcomings - do not account for multicollinearity in the data (Graham 2003; Ray-Mukherjee

379   *et al.* 2014), regression commonality analysis (CA) was applied to disentangle the effect of

380   individual predictors (Newton & Spurrell 1967; Mood 1969, 1971). CA allows to decompose the

381   variance explained by a multiple regression model into unique and common effects of individual

382   predictors (Ray-Mukherjee *et al.* 2014) and has been used in BEF research before (Brooks *et al.*

383   2016). Although CA does not reveal causal relationships between variables, it provides an

384   exploratory tool to partition variance and identify isolated effects as well as groups of covarying

385   predictors. The CA was performed using the R package "yhat" (Nimon, Oswald & Roberts 2013).

386   All analyses were performed in R (R Core team 2015).

Results

2941 grassland plots fulfilled the selection criteria and were included in the analysis. The plots were very unevenly distributed across 9 biomes, with most of the plots located in the temperate midlatitudes (see Table 1). This distribution is a result of the uneven global coverage of sPlot where Europe is highly overrepresented.

Table 1: Number of included plots per biome.
Classifications according to definition by Schultz (2005) with an additional alpine biome following the approach by Körner et al. (2017):

Biome	Number of plots
Alpine	147
Boreal zone	186
Dry midlatitudes	99
Dry tropics and subtropics	264
Polar and subpolar zone	45
Subtropics with winter rain	40
Subtrop. with year-round rain	5
Temperate midlatitudes	2145
Tropics with summer rain	10

Bivariate relationships between single trait functional structure variables and NDVI

The CWMs of most traits were significantly correlated with NDVI. This was tested using simple linear regression analysis with permutation tests. Only the CWMs of the traits Leaf C per mass and height did not have a significant bivariate effect on NDVI. The strongest effect (as R^2) was observed in the simple regression model of the trait SLA, followed by Leaf.N and Stem.Dens (Figure 1).

All the single trait functional diversity values positively correlated to each other (Supplementary material, Table 5) and showed a positive effect on NDVI, exhibiting R^2 values in the range of 0.11 to 0.21 with the strongest effects observed for the traits stem conduit density and stem density (Figure 2).
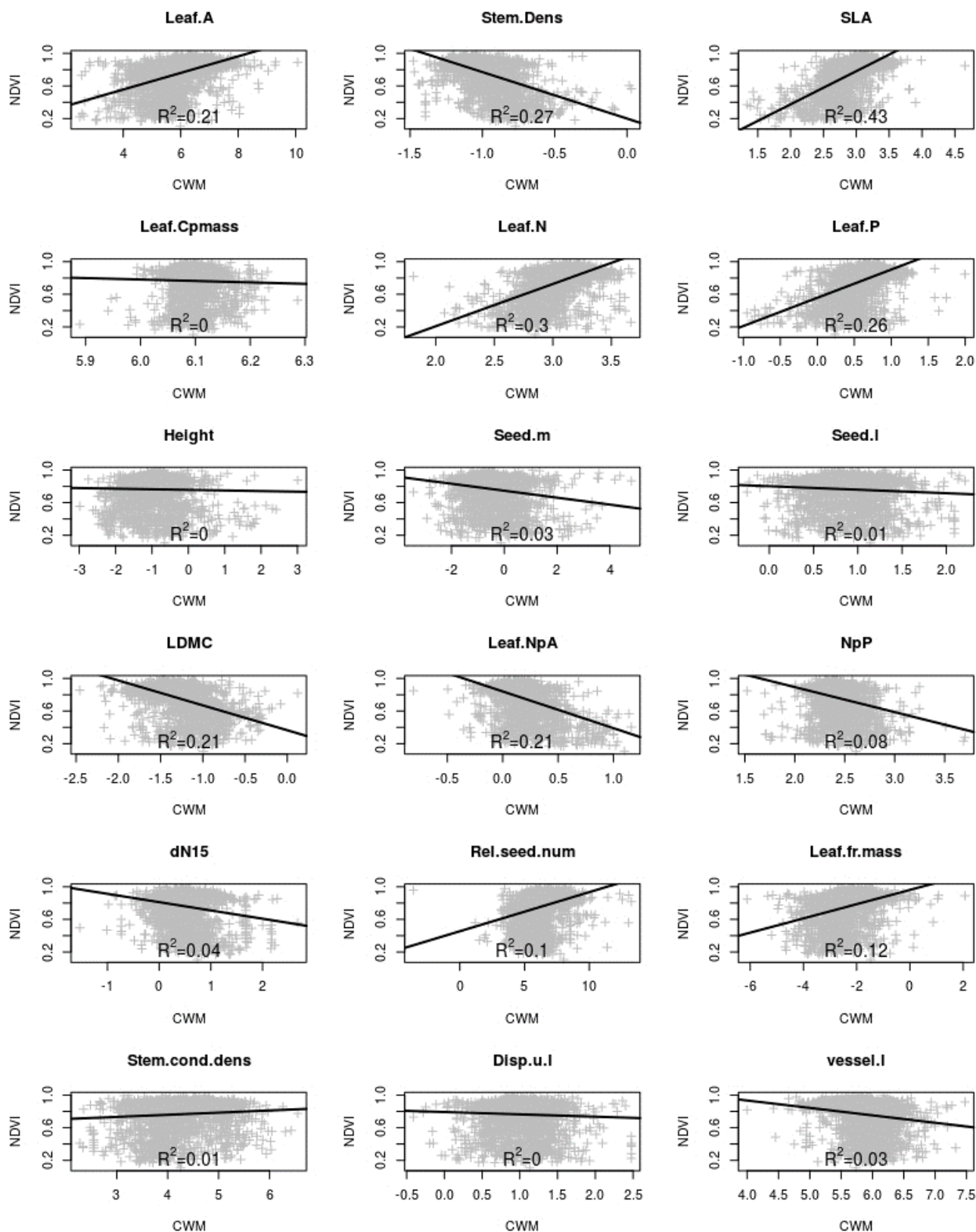
Figure 1: Scatterplots of community weighted mean (CWM) and NDVI for all 18 traits.
Solid lines represent simple linear regression models. R^2 values are given for every fit. Full trait names can be found in Table 2. Apart from the traits Leaf C per mass and height, all CWM had a significant simple regression effect on NDVI.
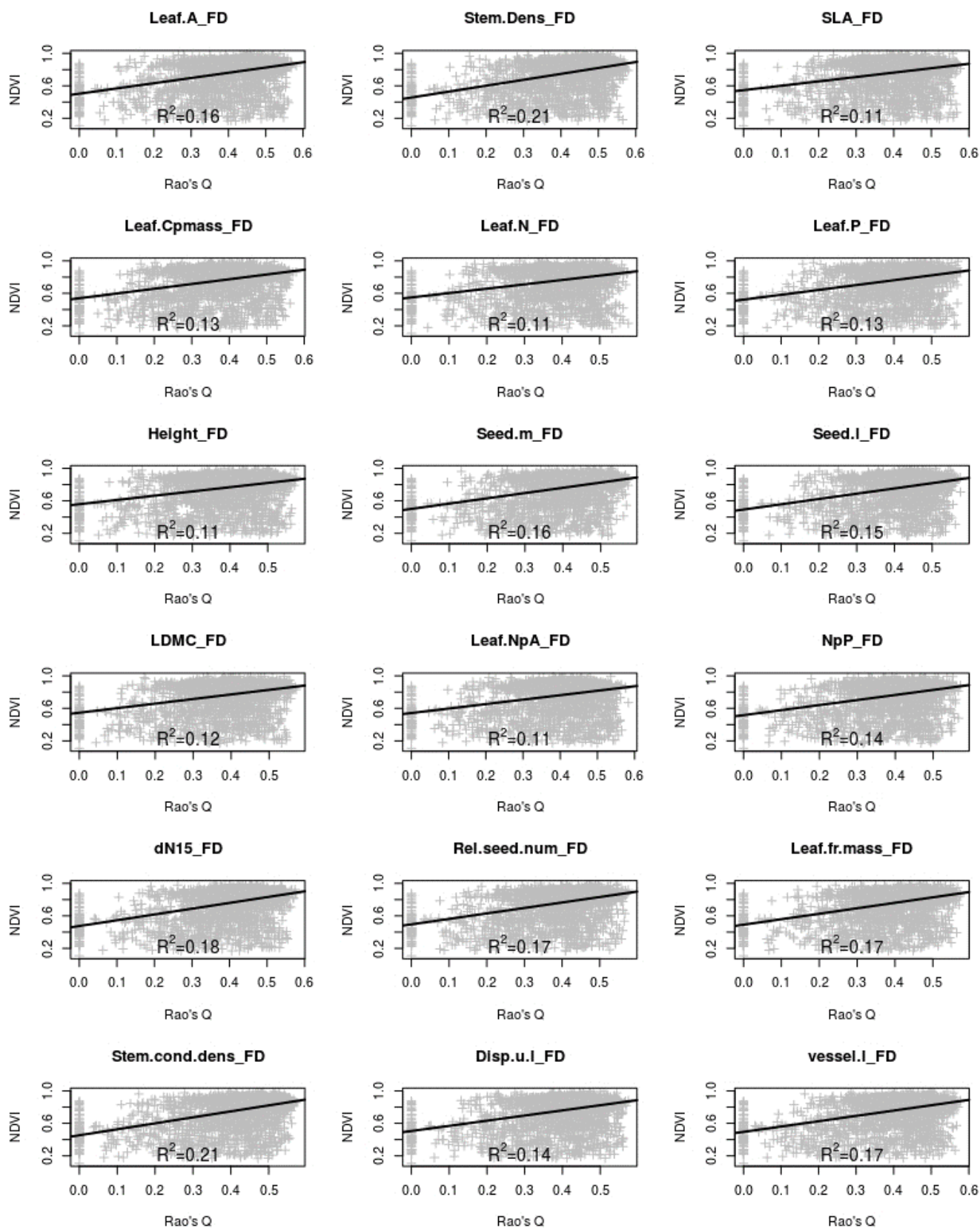
Figure 2: Scatterplots Rao´s quadratic entropy (Q) and NDVI for all 18 traits.
Solid lines represents simple linear regression models. R^2 values are given for every fit. Full trait names can be found in Table 2. All Q values had a significant simple regression effect on NDVI.

The CWM space and its effect on NDVI

403 The first two PCA axes explained 27.42% (PCA.1) and 20.88% (PCA.2) of the variation in the CWM

404 data. Subsequent axes explained 10.2%, 6.5%, 6.3%, 5.4%, 5.1%, 4.3%, 3.3%, 3.1%, 1.9%, 1.8%,

405 1.4%, 0.9%, 0.5%, 0.4%, 0.2% and 0.2%, respectively. Communities that had negative scores on

406 PCA.1 were dominated by species with high SLA that had increased leaf concentrations of

407 nitrogen and phosphorous. Positive values on this axis were accompanied by higher LDMC and

408 stem density. Communities with high scores on the second axis of variation were characterised

409 as dominated by relatively tall species with both, large and heavy leaves and seeds, as well as

410 long dispersal units (see Figure 3 and Table 2). Subsequent axes had relatively low factor

411 loadings; the trait that had the highest correlation with the 3rd axis was dN15 (55,2%), which was

412 in turn not correlated to the first two axes (Table 2).
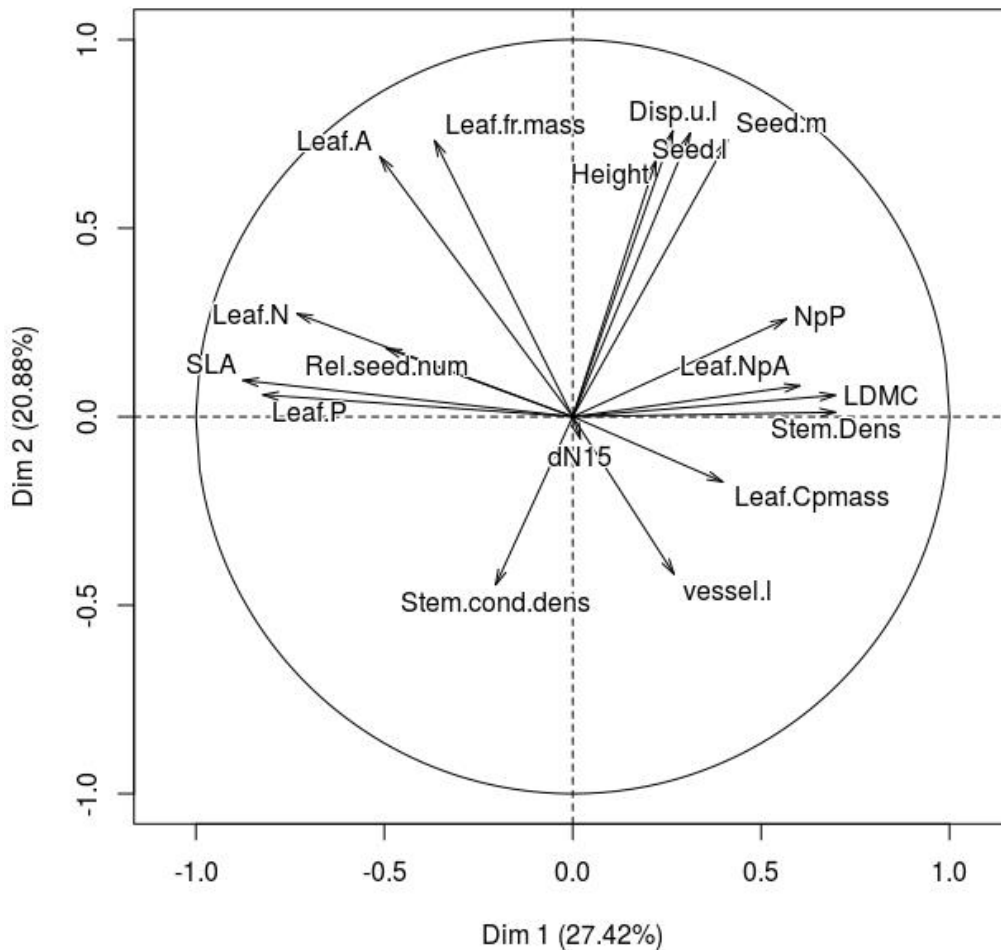
Figure 3: Correlation circle of the CWM PCA for the plane of PCA.1 vs. PCA.2.
Arrows indicating strength and direction of correlation between trait variables and axes. This
plane captures 48.3% of the inertia in the 18 CWM variables. Axis labels Dim 1 and Dim 2 refer
to PCA.1 and PCA.2, respectively.

413 Simple regressions between the PCA axes PCA.1 and PCA.2 and NDVI were significant,
414 respectively. While the first axis showed a relatively strong negative effect, explaining 43% of
415 the variation in NDVI, the second axis had a much smaller but positive effect explaining ca. 2%
416 of the variation (Figure 4).

Table 2: Trait factor loadings on the first 2 PCA axes of the CWM space.
Shading: Red indicates negative correlation, green positive correlation.

Trait	Abbreviation	Correlation with PCA axes	
		PCA 1	PCA 2
Specific leaf area	SLA	-0.88	0.10
Leaf P concentration	Leaf.P	-0.82	0.06
Leaf N concentration	Leaf.N	-0.73	0.27
Leaf area	Leaf.A	-0.51	0.69
Seed number of the reproductive unit	Rel.seed.num	-0.50	0.18
Leaf fresh mass	Leaf.fr.mass	-0.37	0.73
Stem conduit density	Stem.cond.dens	-0.2	-0.45
Leaf delta ^{15}N	dN15	0.02	-0.06
Plant height	Height	0.22	0.68
Dispersal unit length	Disp.u.l	0.27	0.76
Wood vessel length	vessel.l	0.27	-0.42
Seed length	Seed.l	0.31	0.75
Leaf C per dry Mass	Leaf.Cpmass	0.4	-0.17
Seed mass	Seed.m	0.41	0.73
Leaf N/P ratio	NpP	0.57	0.26
Leaf N per Area	Leaf.NpA	0.6	0.08
Leaf dry matter content	LDMC	0.70	0.06
Stem density	Stem.Dens	0.70	0.01
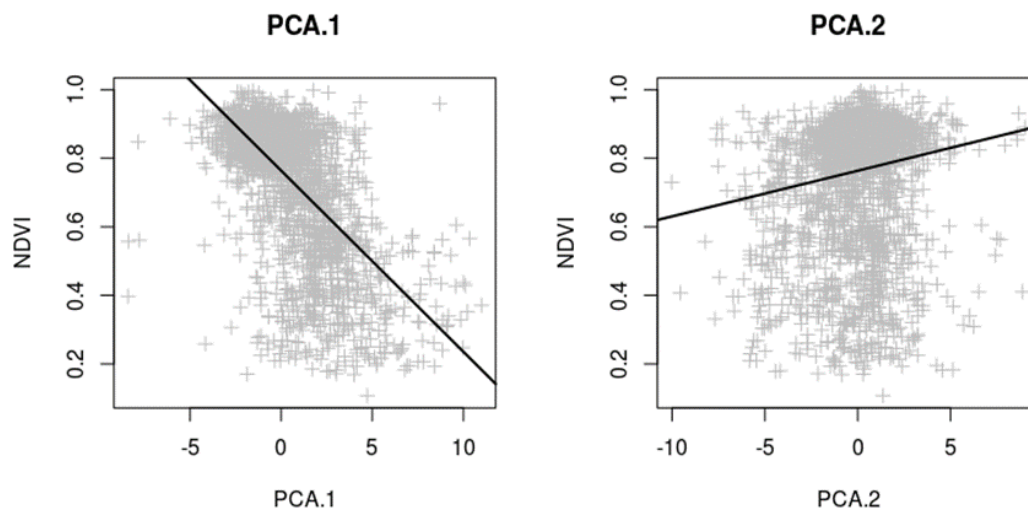
Figure 4: Scatterplot of NDVI against PCA axes of CMW (PCA.1 and PCA.2).
Solid line represents simple linear regression models. R square values are 0.43 and 0.02, respectively. Both models were highly significant as indicated by 5000 randomisations of the data (p<0.001, respectively).

Multiple regression and commonality analysis

The multiple regression model showed that all variables had a significant effect on NDVI, altogether explaining 64.87% of the variation (see Table 3). The commonality analysis revealed how individual predictor variables and sets of predictor variables contributed to this overall R^2 value. The commonality values in Table 3 should be interpreted as follows: The total effect of a variable is equivalent to its R^2 value in a simple linear regression. In the commonality analysis, this value is partitioned into a unique and a common effect of that predictor. The common effect refers to the part of the variation that cannot clearly be attributed to the predictor alone but that is shared with other predictors (due to Multicollinearity). The unique effect, in contrast, is the proportion of the variance in the model that can exclusively be explained by a single predictor. The variable PCA.1 was found to have the highest total effect in the model, the largest part of which, however, was shared with other predictors (37.4%). The unambiguous effect of PCA.1 was 5.2 %. This was the second strongest unique effect of a predictor after the unique effect of precipitation (8.9%). Both, precipitation and latitude had relatively strong total effects with R^2 values of 33.2 % and 25.2%, respectively. While the total effect of FD was 22.8%, only 0.4% where a unique effect of this predictor; the rest was confounded by other covariates. Both, temperature and PCA.2 had relatively weak total effects. In the case of PCA.2, however, its unique effect was stronger than its total effect which suggests that this variable was suppressed by another covariate in the model.

Table 3: Summary of the multiple regression model for NDVI
Unstandardized regression coefficient (B), standardized regression coefficient (β), the number of permutations (Rand); the permutation based p value (p) as well as each predictor's unique, common and total variance in the regression equation.

Variable	B	β	Rand	p	Commonality analysis		
					Unique	Common	Total
PCA.1	-0.024	-0.297	5000	<2e-16	0.052	0.374	0.426
PCA.2	0.019	0.200	5000	<2e-16	0.035	-0.015	0.021
FD	0.140	0.081	5000	<2e-16	0.004	0.224	0.228
Prec	0.061	0.337	5000	<2e-16	0.089	0.244	0.332
Temp	0.043	0.238	5000	<2e-16	0.016	0.017	0.033
Lat	0.008	0.472	5000	<2e-16	0.044	0.208	0.252

Adjusted R^2 = 0.6487; Intercept = 0.764

Table 4 summarises the contribution of individual predictor sets ordered by effect size. The set of variables with the highest commonality coefficient was the predictor set "PCA.1, FD, Prec, and Lat" which can be attributed 14.2% of the total regression effect. The variable PCA.1 was part of 6 out of the 8 most important predictor sets and shared most of its total effect with the covariates precipitation and latitude. Furthermore, PCA.1 had some shared model variation with the functional diversity value FD.

Table 4: Contribution of predictors and predictor sets on NDVI.
The table shows commonality coefficients and % of total contribution of each predictor or predictor set to the regression effect in decreasing order. Sets with contributions below 2% were omitted in this table.

Set of variables	Coefficient	% Total
PCA.1, FD, Prec, and Lat	0.092	14.2
Prec	0.089	13.66
PCA.1, and Lat	0.08	12.25
PCA.1, and Prec	0.056	8.57
PCA.1	0.052	7.96
Lat	0.044	6.84
PCA.1, Prec, and Lat	0.044	6.76
PCA.1, FD, and Lat	0.043	6.62
PCA.2	0.035	5.41
FD, and Lat	0.026	3.98
FD, Prec, and Lat	0.021	3.19
PCA.1, and Temp	0.021	3.17
PCA.1, FD, Prec, and Temp	0.018	2.78
PCA.1, Prec, and Temp	0.018	2.74
Temp	0.016	2.47
FD, and Prec	0.015	2.29
…47 sets with contribution below 2 % omitted…		
Total	0.649	100

442

Discussion

The aim of the present study was to provide a global assessment of the role of dominance and complementarity effects for biodiversity – ecosystem functioning relationships in grasslands. Functional community structure was described by two components, functional diversity (FD) and community weighted mean (CWM), which were associated with complementarity and dominance effects, respectively. Prior to the discussion of the trait - functioning relationships which has been considered a "holy grail" in ecology (Lavorel & Garnier 2002), the associations among CWM of different traits will be discussed in the next section. At the end of this paper, some methodological considerations will be presented.

The CWM space

Although 18 different traits were used in this study, the PCA of the CWM revealed that there were in fact only two main axes that explained almost half of the variation in the CWM data and that many traits were tightly linked to. A full pairwise correlation matrix of the CWMs can be found in the Supplementary material (Table 5, Figure 6). In the following, interpretations of the first two PCA axes will be provided.

From leaf economics to community economics

PCA.1 combined traits that were associated to the leaf economics spectrum (Wright *et al.* 2004). Negative values on this axis can be interpreted as communities dominated by "acquisitive species" (high SLA, Leaf.P, Leaf.N), whereas positive scores indicate domination by "conservative species" (high LDMC). This axis PCA.1 is analogous to the well-known LES described by many studies (Chapin 1980; Reich, Walters & Ellsworth 1997; Wilson, Thompson & Hodgson 1999; Wright *et al.* 2004; Díaz *et al.* 2016). The fact that not only leaf traits, but also the trait stem density is strongly correlated to this axis supports the notion of a "Plant economics spectrum" beyond leaf traits (Freschet *et al.* 2010). This idea that traits are coordinated at the plant level between different organs (e.g. leaves, stem, roots) represents a paradigm shift that has gained more and more attention in recent years (Freschet *et al.* 2013; Laughlin 2014; Reich 2014). The results of this study support this idea suggesting that communities on the conservative side of the LES also exhibit higher stem densities: This represents two sides of the same coin which is a "fast-slow" plant economics spectrum (Reich 2014). Numerous studies found that such cross-organ trait associations and trait-environment links are stronger when measured at the community level (as CWM) than at the species level (as species trait values) (Ackerly *et al.* 2002; Cingolani *et al.* 2007; Domínguez *et al.* 2012; de la Riva *et al.* 2016). This supports the theory that dominant species in a community are more strongly affected by environmental filters and

476 constraints than less abundant species (de la Riva *et al.* 2016). Furthermore, this finding has

477 inspired the concept of a "plant community economics spectrum" as an extension of the "plant

478 economics spectrum" (Pérez-Ramos *et al.* 2012) emphasising the community level trait variation

479 and both, its responses to environmental filters and its effects on ecosystem processes

480 (Domínguez *et al.* 2012; de la Riva *et al.* 2016; Jiang *et al.* 2017). The methodology adopted in

481 this study followed the community level approach by performing the PCA on the CWM values

482 as opposed to using trait values measured at the individual or species level. Hence, the axis

483 PCA.1 should be interpreted as a community level resource acquisition–conservation trade-off

484 following the logic of Pérez-Ramos *et al.* (2012).

485 *On leaves and seeds*

486 The second axis of variation PCA.2 summarizes variation in CWM of leaf size and weight, plant

487 height and seed traits. Although, at species level, plant size and reproductive traits are expected

488 to be independent according to the LHS scheme (Westoby 1998), at community level both trait

489 groups load on the second PCA axis in this study. This is in accordance with other studies that

490 provide evidence suggesting that large plants have larger seeds (Thompson & Rabinowitz 1989).

491 However, it is arguable if the combination of leaf area and leaf fresh mass with the seed traits

492 within this axis represent a true ecological spectrum or if this is rather a forced marriage caused

493 by the ordination technique. The pairwise correlation between the traits seed mass and leaf

494 area was with 0.29 (Pearson's R) not exactly strong. As seen in Figure 3, both traits were at either

495 side of the PCA.2 axis pulling it in opposite directions along the horizontal axis despite high

496 individual loadings on PCA.2. Therefore, the mutual axis of leaf traits and seed traits does not

497 necessarily represent a true ecological convergence but rather a weak allometric correlation

498 that gets overrepresented due to the rotation of the CWM space by the PCA. The fact that the

499 traits leaf fresh mass and leaf area also cross load on PCA.1 (see Figure 3) and that they are

500 correlated with SLA seems to challenge the notion that SLA and leaf area are independent

501 (Ackerly & Reich 1999; Fonseca *et al.* 2000). For instance, in the recently compiled "global

502 spectrum of plant form and function", leaf area and leaf mass per area (i.e. the inverse of SLA)

503 form almost orthogonal axes in the 2 dimensional trait space (r^2 = 0.01; Díaz *et al.* 2016).

504 However, as shown by Ackerly *et al.* (2002), this independence is only found at the species level.

505 For CWM their findings show that "at the community level, the parallel shifts [along an

506 environmental gradient] in mean leaf size and mean SLA led to a very strong correlation between

507 the two" (Ackerly *et al.* 2002). The community based approach adopted here confirms these

508 findings as there was moderate correlation between the CWMs of SLA and leaf area (Pearson's

509 R = 0.45). This indicates, that leaf area and SLA have a certain degree of convergence for the

510 dominant species in a plant community, which are most affected by environmental filters. In
511 effect, the results suggest that leaf area might contribute to the "plant community economics
512 spectrum" proposed by Pérez-Ramos *et al.* (2012).

Effects on NDVI

514 NDVI was used as a measure of ecosystem functioning in this study and a multiple regression
515 analysis was applied to evaluate how it was affected by different components of plant functional
516 community structure and abiotic factors. Ca. 65 % of the variation in NDVI was explained by the
517 predictor variables, which represents a relatively high explanatory power of the global model
518 given the relative "roughness" of the methodology applied and the neglection of potentially
519 important covariates (see Methodological considerations). The fact that all predictor variables
520 were statistically highly significant should not be overrated in this context, for this is a common
521 occurrence with large sample sizes (Lantz 2013; Khalilzadeh & Tasci 2017). The following sections
522 will consider the effects that were attributed to the individual predictor variables and discuss
523 underlying mechanisms.

Dominance vs. complementarity

525 Whether biodiversity influences ecosystem processes through the traits of the most dominant
526 species in a community or through non-additive complementarity effects has been a widely
527 studied question for a range of different systems, taxa and ecosystem processes (Cornwell *et al.*
528 2008; Lavorel 2013; Brooks *et al.* 2016).

529 For plant communities, there is striking evidence that dominant species determine ecosystem-
530 level productivity through their traits of resource economics (Lavorel 2013). Also, the results of
531 this study strongly support this theory: The latent variable PCA.1 which represents a "plant
532 community economics spectrum" calculated from CWM trait values (Pérez-Ramos *et al.* 2012)
533 had the highest overall effect on the NDVI response and shared 2/3 of the total explained
534 variation in the model. Even its isolated effect was relatively strong compared to the other
535 predictors. The importance of this variable can be explained by the "fast-slow continuum" that
536 it describes. Communities that are dominated by acquisitive species are at the "fast" side of the
537 spectrum because they generally exhibit fast growth and rapid C and N turnover. This entails
538 high rates at the ecosystem level for instance in terms of biomass accumulation, decomposition
539 and evapotranspiration (Reich 2014). Likewise, the NDVI metric was very responsive to this axis.
540 This is not very surprising since the annual peak NDVI value which was used here represents the
541 high productivity season with an expected maximum resource turnover (Pettorelli *et al.* 2005).
542 The second PCA axis had a weak positive effect on NDVI. As discussed earlier, it lumped together

543   leaf and seed traits with height which did not all have a strong correlation between them

544   (Supplementary material, Figure 6). It is striking that their single regression effects are in

545   opposite directions, with leaf area showing a strong positive association and seed mass a weak

546   negative association with NDVI (Figure 1). This emphasises the earlier notion that this set of

547   traits is not converging. However, the NDVI gradient that is here referred to cannot be thought

548   of as an environmental filter but rather describes an effect of the plant community on ecosystem

549   processes (Pillar *et al.* 2009). As result of the lack of sound ecological meaning of the PCA.2

550   variable, it does not make sense to consider its dominance effect on ecosystem functioning. Yet,

551   one should note that the trait plant height, which was also correlated to this axis had no bivariate

552   effect on NDVI (Figure 1). This suggests that the plant size axis of trait variation (Westoby 1998),

553   is not relevant for productivity in the grassland systems under study.

554   The effect of plant functional diversity on ecosystem processes is not consistent in the literature.

555   Some studies found positive (Mouillot *et al.* 2011), some negative (Thompson *et al.* 2005), some

556   no association (Chollet *et al.* 2014). The results of the present study show a tendency for a

557   positive effect: The FD predictor variable had a moderate total effect on NDVI. Yet, almost no

558   variation was explained by it alone. Notably, FD shared a large portion of its explanatory power

559   with the dominance indicator PCA.1. This was not unexpected as the metrics CWM and FD are

560   not independent of each other (Ricotta & Moretti 2011; Dias *et al.* 2013). Furthermore, high

561   productivity systems are expectedly allowing for more diversity, which means that causality

562   could also flow from NDVI to FD. As no causal modelling was applied here, one cannot identify

563   a definite complementarity effect. It was remarkable, however, that all single trait Q values had

564   consistently positive bivariate effects on NDVI, which suggests that the traits diverge equally

565   along the NDVI gradient. The single trait Q variables with the highest effect on NDVI belonged

566   to the traits stem density and stem conduit density (both were combined for the calculation of

567   FD). Those traits play a crucial role in plant water conductivity and evapotranspiration (Zanne *et*

568   *al.* 2010). Accordingly, a potential effect of FD could be explained by complementarity along the

569   water resource axis. A positive effect of complementarity in water use strategies on biomass

570   production in grasslands has been reported by Verheyen *et al.* (2008). As both, water and carbon

571   fluxes are controlled by stomatal conductance, photosynthesis is tightly linked to transpiration

572   and water use in plants (Jarvis & Davies 1998). This link is also manifested in the response

573   variable NDVI which is an indicator of both, productivity and evapotranspiration at the

574   ecosystem level (Chong, Mougin & Gastelluetchegorry 1993). To further explore the role of

575   niche differentiation of water use, it would be helpful to have information on root traits which

576   is currently still scarce in TRY (Kattge *et al.* 2011). While there was an indication for a potential

577 effect of complementarity, the results of this study strongly suggest that for the annual peak
578 NDVI value dominance effects constitute the most important BEF mechanism in grasslands. As
579 previous work shows that complementarity effects might be stronger outside of the high
580 productivity season (Chollet *et al.* 2014), it is possible that FD is more important for NDVI values
581 that do not correspond to the annual maximum.

582 *The role of covariates*

583 Ecosystem processes result from a complex interplay of abiotic and biotic factors and in return
584 affect both, the environment and biological communities through global feedback loops (Chapin
585 *et al.* 2000). As effect and response traits are tightly linked within a community (Lavorel &
586 Garnier 2002), the influence of plant functional community structure on productivity should be
587 discussed in the light of environmental factors if they are not experimentally controlled for. In
588 grasslands, climate is one of the major drivers of productivity. La Pierre *et al.* (2011) found that
589 during high productivity seasons precipitation was a strong predictor of aboveground biomass
590 production in a mesic grassland. This finding was reproduced by the present study: Annual total
591 precipitation had high predictive power for annual peak NDVI and exhibited the strongest
592 isolated effect of all variables (Table 3). Notably, precipitation also shared considerable part of
593 its contribution to the NDVI variation with PCA.1 and FD which suggests its effect could at least
594 partly be mediated by the plant community (Figure 5). A negative correlation between
595 precipitation and PCA.1 indicates that communities in locations with high precipitation tend to
596 be dominated by "acquisitive species" entailing higher NDVI values through the dominance
597 effect. This mechanism of mediation is plausible because the "slow-fast continuum" described
598 by PCA.1 is known to be linked to drought tolerance strategies whereby slow/ conservative
599 species show greater success under arid conditions (Reich 2014). Also at the community level,
600 the plant economics spectrum was reported to converge along a gradient of soil water content
601 (de la Riva *et al.* 2016). The second possible pathway of mediation is linked to the
602 complementarity effect: At higher water availability levels (Prec), one can expect a wider niche
603 space along the water resource axis and weaker environmental constraints which leads to higher
604 differentiation of water use strategies (divergence) and complementarity effects as discussed
605 above. Medium correlations between Prec, FD and NDVI support this theory (Figure 5).
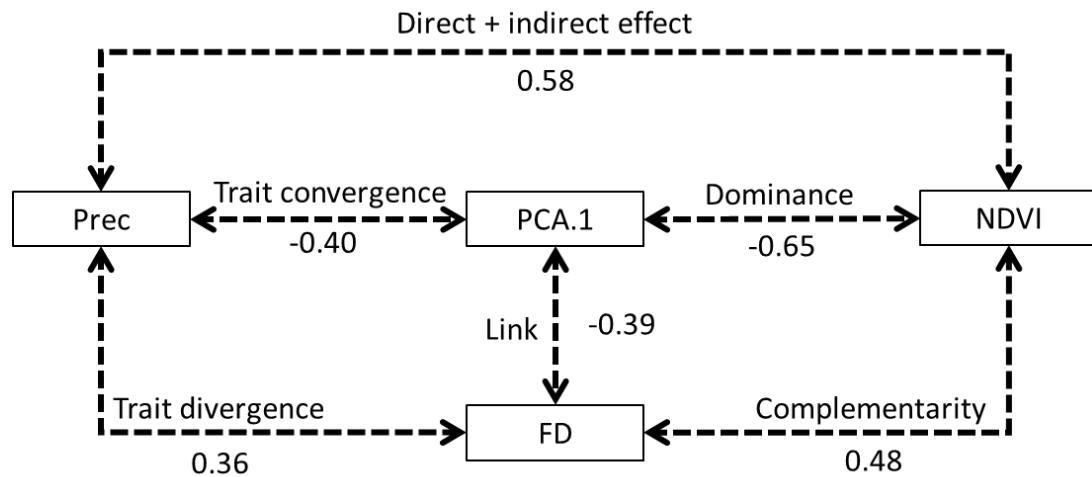
Figure 5: Pairwise Pearson correlations between Prec, PCA.1, FD and NDVI.
Potential underlying mechanisms are shown as arrows. Note that this is not a valid causal model but just an overview of resemblance between variables.

606 The fact that the variable temperature only had a minor effect on NDVI seems to contradict

607 widely accepted findings that attribute an important role to this factor (Briggs & Knapp 1995).

608 Recent findings, however, show that timing is crucial for the effect of temperature in grasslands.

609 While the temperature at the beginning of the growing season was reported to be most

610 important for annual biomass production (Chollet *et al.* 2014; Guo *et al.* 2017), the temperature

611 variable used here, does not account for this temporal variability: The annual mean temperature

612 (calculated across many years) was not very important in the model. This suggest that

613 microvariation in temperature might be much more important than global temperature

614 gradients. As expected, temperature was strongly correlated to latitude (Pearson's r = 0.80).

615 Interestingly, latitude had a relatively strong effect on NDVI that was not common to

616 temperature (Table 3). Thus, the latitudinal gradient of NDVI must be related to other variables

617 changing with latitude such as solar radiation and seasonality.

618 Methodological considerations

619 The data-driven approach presented in this study is novel in the context of BEF research. Using

620 a vegetation plot database has the striking advantage that a vast number data points can be

621 included and that available ecological information is reused (the current version of sPlot holds

622 more than 1.1 million plots). Consequently, one can increase both, spatial and temporal extent

623 of the study far beyond what is feasible with new data collection. However, this approach also

624 comes with a trade-off: As the information compiled in the databases was not collected to

625 address the specific question of the study, the data might not be good enough to resolve the

626 relevant ecological patterns and processes or - even worse - be extremely biased. While the aim

627 of this study was to investigate the role of plant functional community structure, the plant
628 surveys that contribute to sPlot only report species composition. To overcome this limitation,
629 the community matrix was matched with trait information from the trait database TRY. Hence,
630 the functional community structure was approximated using trait mean values from plants
631 collected by different botanists at potentially very different locations. Not only does this
632 procedure neglect inherent intraspecific trait variation but also it does ignore the local
633 environmental conditions and resources that individuals in a community respond to (phenotypic
634 plasticity). Accordingly, it was found that trait databases only had a limited power to predict trait
635 composition at the plot level in a European saltmarsh (Cordlandwehr *et al.* 2013). Yet, one can
636 argue that if ecological patterns are strong enough they can nonetheless be resolved with a
637 sufficient number of data points even if those are unprecise. Hortal *et al.* (2014) discuss the
638 manifold shortcomings of big data in ecology. Pressing the scientific community to fill the
639 extensive gaps in the data and carefully consider limitations, they close their review with the
640 following quote by Daniel J. Boorstin (1983): "The greatest enemy of knowledge is not ignorance,
641 it is the illusion of knowledge."

642 There is no doubt that the approach adopted in this study has some substantial limitations that
643 surely introduce biases. Not only does the use of trait databases lead to a very rough
644 approximation of functional community structure but also the vegetation plot database did have
645 vast gaps in its global coverage. As shown in Table 1, almost ¾ of the plots included in this study
646 are in the temperate midlatitudes (mainly Europe, partly Australia), which introduces a major
647 bias. Especially, South America and Africa were underrepresented in this "global" compilation
648 (see Supplementary material, Figure 7). Furthermore, there was a substantial scale
649 incompatibility between the vegetation surveys and the NDVI measure: The MODIS product
650 MOD13Q1 that was considered the best compromise in the trade-off between temporal
651 coverage and spatial resolution is with its pixel size of 250 m roughly 2 orders of magnitude
652 coarser than a typical vegetation plot. The use of the landcover map surely mitigates this
653 problem to a certain degree but it does not represent a true scaling from plot to ecosystem level
654 (Reichstein *et al.* 2014). For both, NDVI and climatic variables microvariation (e.g. temporal
655 variability and microclimate) was neglected in this study. Furthermore, other crucial factors to
656 grassland dynamics such as nutrient availability, soil properties and disturbances regimes (e.g
657 grazing, fire and flooding) were ignored. Future efforts will have to be undertaken to face this
658 ignorance by including more data, and more comprehensive analysis techniques will have to be
659 applied to treat the uncertainty and biases of this study.

660 Are the results of this study a valid contribution to the BEF debate despite the methodological

661 shortcomings? The model that was built here showed a relatively high overall fit of the data

662 which suggests that at least some of the most important factors of grassland dynamics have

663 been included. The total contribution of the dominance effect, for instance, was larger than the

664 residual variation of the model, which strongly supports the mass ratio hypothesis suggesting

665 that dominant trait values are driving a global productivity gradient across these grassland

666 communities. Complementarity effects were rather subtle but the data show that especially in

667 response to precipitation, niche differentiation along the water use axis might play a

668 considerable role. These findings are neither surprising (as they are strongly echoing in the

669 literature) nor do they have direct consequences for management (they are mainly theory

670 driven). Hence, there is no major damage done in reporting them and discussing them in the

671 face of their limitations. The novel approach discussed in this paper represents - along with other

672 studies along these lines (e.g. Musavi *et al.* 2016, 2017; Spasojevic *et al.* 2016) a step forward

673 towards more integrative data-driven biodiversity ecosystem functioning debate at the global

674 scale.

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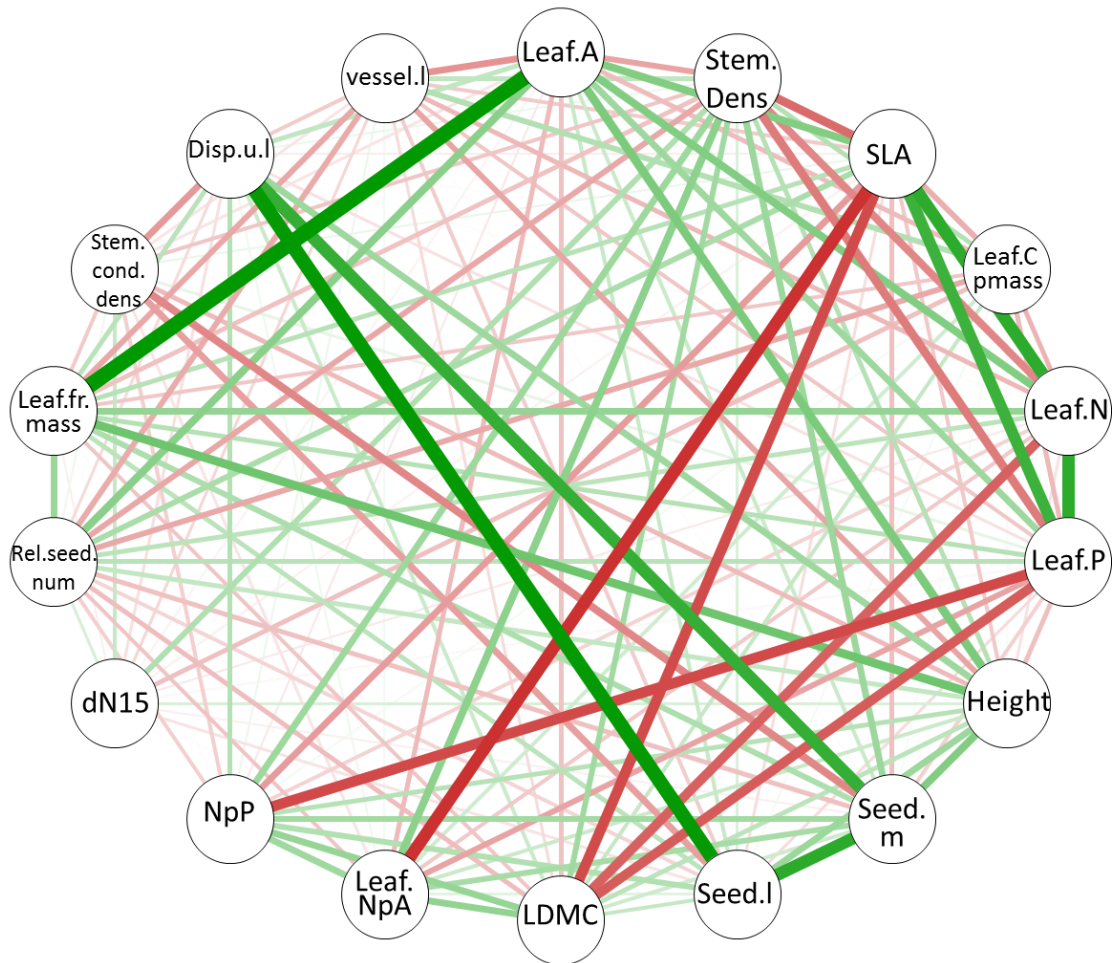
Supplementary material

Figure 6: Correlation network of all 18 CWM values.
Width of line between two traits is proportional to their pairwise Pearson correlation coefficient. Green stands for positive, red stands for negative correlation. This graphic was produced using the R package "qgraph".

Table 5: Pairwise Pearson correlation between traits.
Shown are correlations among CWM (upper triangular matrix) and Q (lower triangular matrix) of all 18 trait. This legend defines the upper side of the matrix.

| FD\CWM	Leaf.A	Stem.Dens	SLA	Leaf.Cpmass	Leaf.N	Leaf.P	Height	Seed.m	Seed.l	LDMC	Leaf.NpA	NpP	dN15	Rel.seed.num	Leaf.fr.mass	Stem.cond.den	Disp.u.l	vessel.l
Leaf.A	1.00	-0.33	0.45	-0.24	0.45	0.35	0.47	0.19	0.20	-0.22	-0.25	-0.08	-0.04	0.42	0.92	-0.09	0.22	-0.39
Stem.Dens	0.82	1.00	-0.53	0.27	-0.43	-0.47	0.27	0.36	0.14	0.34	0.42	0.35	0.28	-0.32	-0.22	-0.21	0.07	0.23
SLA	0.78	0.78	1.00	-0.29	0.75	0.70	-0.20	-0.23	-0.12	-0.65	-0.74	-0.35	-0.05	0.30	0.26	0.08	-0.07	-0.19
Leaf.Cpmass	0.78	0.80	0.76	1.00	-0.27	-0.25	0.03	0.03	0.04	0.20	0.17	0.04	-0.23	-0.31	-0.20	0.01	0.02	0.28
Leaf.N	0.77	0.80	0.78	0.80	1.00	0.76	-0.10	-0.01	0.00	-0.57	-0.19	-0.16	-0.08	0.25	0.38	0.01	0.02	-0.26
Leaf.P	0.80	0.81	0.77	0.78	0.80	1.00	-0.23	-0.17	-0.13	-0.59	-0.33	-0.65	-0.03	0.25	0.27	0.09	-0.11	-0.21
Height	0.78	0.79	0.73	0.71	0.73	0.74	1.00	0.45	0.36	0.24	0.19	0.26	0.14	0.21	0.52	-0.25	0.35	-0.32
Seed.m	0.77	0.79	0.75	0.72	0.74	0.76	0.79	1.00	0.76	0.18	0.32	0.33	-0.05	-0.22	0.30	-0.43	0.73	-0.02
Seed.l	0.80	0.82	0.81	0.77	0.79	0.79	0.79	0.88	1.00	0.21	0.10	0.28	-0.10	-0.15	0.24	-0.34	0.91	-0.18
LDMC	0.80	0.78	0.77	0.75	0.77	0.79	0.75	0.77	0.79	1.00	0.39	0.38	-0.01	-0.24	-0.21	0.00	0.19	-0.13
Leaf.NpA	0.80	0.81	0.85	0.80	0.81	0.79	0.75	0.78	0.83	0.78	1.00	0.34	0.02	-0.21	-0.02	-0.09	0.06	0.04
NpP	0.78	0.82	0.74	0.76	0.81	0.83	0.75	0.77	0.81	0.75	0.80	1.00	0.01	-0.17	-0.02	-0.17	0.27	0.07
dN15	0.81	0.81	0.77	0.77	0.77	0.81	0.73	0.78	0.80	0.78	0.79	0.79	1.00	0.14	-0.06	0.21	-0.11	-0.15
Rel.seed.num	0.78	0.81	0.75	0.75	0.76	0.77	0.77	0.80	0.79	0.75	0.77	0.77	0.79	1.00	0.36	0.06	-0.13	-0.30
Leaf.fr.mass	0.95	0.83	0.79	0.78	0.78	0.80	0.78	0.79	0.81	0.80	0.81	0.78	0.81	0.79	1.00	-0.19	0.25	-0.32
Stem.cond.dens	0.80	0.86	0.77	0.78	0.79	0.80	0.77	0.78	0.82	0.77	0.81	0.81	0.80	0.78	0.82	1.00	-0.37	-0.09
Disp.u.l	0.80	0.79	0.80	0.77	0.79	0.78	0.77	0.85	0.95	0.78	0.82	0.79	0.80	0.77	0.80	0.81	1.00	-0.19
vessel.l	0.81	0.82	0.77	0.79	0.78	0.80	0.76	0.78	0.81	0.80	0.80	0.82	0.80	0.80	0.81	0.81	0.81	1.00
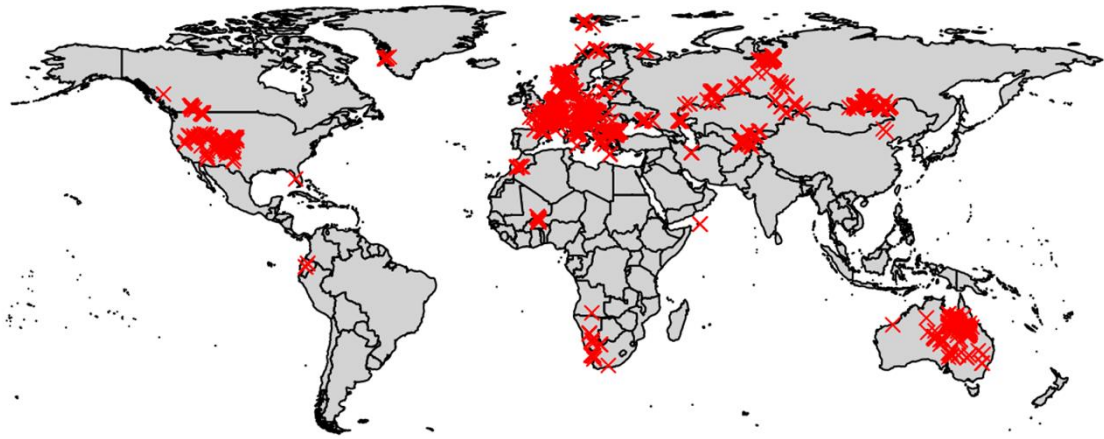
Figure 7: Locations of the 2941 observations included in the analysis.

Table 6: Pairwise Pearson correlation between model variables.

	NDVI	PCA.1	PCA.2	FD	Temp	Prec	Lat
NDVI_max	1	-0.653	0.143	0.477	-0.182	0.576	0.502
PCA.1	-0.653	1	0	-0.386	0.24	-0.404	-0.519
PCA.2	0.143	0	1	-0.114	0.329	-0.017	-0.254
FD	0.477	-0.386	-0.114	1	-0.234	0.362	0.504
Temp	-0.182	0.24	0.329	-0.234	1	-0.056	-0.798
Prec	0.576	-0.404	-0.017	0.362	-0.056	1	0.226
Lat	0.502	-0.519	-0.254	0.504	-0.798	0.226	1