

# Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality

Yoann Le Bagousse-Pinguet<sup>a,b,1,2</sup>, Santiago Soliveres<sup>c,d,1,2</sup>, Nicolas Gross<sup>a,e,1,2</sup>, Rubén Torices<sup>a,f</sup>, Miguel Berdugo<sup>a</sup>, and Fernando T. Maestre<sup>a</sup>

<sup>a</sup>Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain; <sup>b</sup>Aix Marseille University, University of Avignon, CNRS, Institut de Recherche pour le Développement, Institut Méditerranéen de Biodiversité et d'Écologie marine et continentale, F-13545 Aix-en-Provence cedex 04, France; <sup>c</sup>Departamento de Ecología, Universidad de Alicante, 03690 Alicante, Spain; <sup>d</sup>Instituto Multidisciplinar para el Estudio del Medio Ramón Margalef, Universidad de Alicante, 03690 Alicante, Spain; <sup>e</sup>Univ Clermont Auvergne, Institut National de la Recherche Agronomique, VetAgro Sup, UMR Écosystème Prairial, 63000 Clermont-Ferrand, France; and <sup>f</sup>Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, 04120 Almería, Spain

Edited by Nils C. Stenseth, University of Oslo, Oslo, Norway, and approved March 12, 2019 (received for review September 11, 2018)

**Biodiversity encompasses multiple attributes such as the richness and abundance of species (taxonomic diversity), the presence of different evolutionary lineages (phylogenetic diversity), and the variety of growth forms and resource use strategies (functional diversity). These biodiversity attributes do not necessarily relate to each other and may have contrasting effects on ecosystem functioning. However, how they simultaneously influence the provision of multiple ecosystem functions related to carbon, nitrogen, and phosphorus cycling (multifunctionality) remains unknown. We evaluated the effects of the taxonomic, phylogenetic, and functional attributes of dominant (mass ratio effects) and subordinate (richness effect) plant species on the multifunctionality of 123 drylands from six continents. Our results highlight the importance of the phylogenetic and functional attributes of subordinate species as key drivers of multifunctionality. In addition to a higher taxonomic richness, we found that simultaneously increasing the richness of early diverging lineages and the functional redundancy between species increased multifunctionality. In contrast, the richness of most recent evolutionary lineages and the functional and phylogenetic attributes of dominant plant species (mass ratio effects) were weakly correlated with multifunctionality. However, they were important drivers of individual nutrient cycles. By identifying which biodiversity attributes contribute the most to multifunctionality, our results can guide restoration efforts aiming to maximize either multifunctionality or particular nutrient cycles, a critical step to combat dryland desertification worldwide.**

functional diversity | mass-ratio hypothesis | nutrient cycling | phylogenetic diversity | taxonomic diversity

Understanding the relationship between biodiversity and the capacity of ecosystems to perform multiple functions simultaneously (multifunctionality) has been a core ecological research topic in the last decade (1–4). In recent years, considerable research efforts have been devoted to explore how the biodiversity–ecosystem multifunctionality relationship (B–EMF relationship) is contingent upon the number and identity of ecosystem functions considered (e.g., refs. 5 and 6). In contrast, how multiple attributes of biodiversity such as the richness and abundance of species (taxonomic diversity) and the diversity of evolutionary lineages (phylogenetic diversity) and that of the traits related to resource use strategy (functional diversity) simultaneously influence ecosystem functioning remains poorly investigated (7–11), particularly at the global scale. Since these biodiversity attributes do not necessarily correlate (12, 13), assessing how they simultaneously influence multifunctionality is crucial not only to expand our fundamental understanding of the B–EMF relationships but also to prioritize relevant biodiversity attributes in global conservation programs and to improve management actions to preserve and restore terrestrial ecosystems (12, 14).

While most B–EMF studies have focused on species richness (1–3), functional diversity is also a key driver of multifunctionality (15–17). Higher functional diversity could enhance multifunctionality either because co-occurring species with contrasting trait values increase the overall resource utilization (18) or by including species that strongly affect ecosystem functioning (sampling effect; ref. 19). The phylogenetic diversity of plant communities can also influence ecosystem functions such as biomass production (7, 8). However, how phylogenetic diversity influences the B–EMF relationships remains unclear (20), and we do not know whether early diverging vs. recent evolutionary events ultimately influence ecosystem functioning (21). Phylogenetic diversity is a key biodiversity attribute when it effectively encompasses unmeasured biological traits that are relevant for ecosystem functioning (7, 22). As such, considering simultaneously phylogenetic diversity, which often grasps traits that are not typically measured [e.g., those related to plant–pathogen or plant–mycorrhiza interactions (23, 24)], and

## Significance

**Biodiversity is declining globally, but its different taxonomic, functional, and evolutionary attributes are doing so at a different pace. Understanding how these attributes influence ecosystem functioning is crucial to better predict the ecological consequences of biodiversity loss. Based on a survey of 123 drylands worldwide, our results highlight the phylogenetic and functional attributes of subordinate species as key drivers of the provision of multiple ecosystem functions simultaneously (multifunctionality). Our study expands our understanding of the relationship between biodiversity and multifunctionality by identifying the diversity of early diverging lineages and functional redundancy as important biodiversity attributes to prioritize in conservation and restoration programs aimed at promoting dryland multifunctionality worldwide.**

Author contributions: Y.L.B.-P., S.S., N.G., and F.T.M. designed research; Y.L.B.-P., S.S., and N.G. performed research; R.T. and M.B. contributed analytic tools; F.T.M. coordinated data acquisition; Y.L.B.-P. analyzed data; and Y.L.B.-P., S.S., N.G., R.T., M.B., and F.T.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

Data deposition: Data are available through the Figshare repository, <https://figshare.com/s/08b538101fe252a2e879>, <https://figshare.com/s/5c951b7f82dd551737b8>.

<sup>1</sup>Y.L.B.-P., S.S., and N.G. contributed equally to this work.

<sup>2</sup>To whom correspondence may be addressed. Email: yoann.pinguet@imbe.fr, santiagosoliverescodina@gmail.com, or nicolas.gross@inra.fr.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1815727116/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1815727116/-DCSupplemental).

Published online April 4, 2019.

measured traits could better account for the many dimensions of trait diversity exhibited by plant species (7, 13). Therefore, doing so could provide greater insights on how the multidimensionality of biodiversity influences multifunctionality.

No matter the taxonomic, phylogenetic, or functional attribute of biodiversity we look at, focusing solely on richness ignores the overwhelming effect that dominant species may have on ecosystem functioning (25, 26). According to the mass ratio hypothesis (25), the effect of plant species on ecosystem functioning is directly proportional to their biomass (mass ratio effects) and thus is relatively insensitive to the richness of subordinate species (25). This hypothesis was originally framed for individual functions related to biomass production and carbon cycling (25–27). However, the importance of the dominant species seems less clear when focusing on multifunctionality (28, 29) as it may depend on the attribute of biodiversity or the function considered.

To better understand the functional consequences of biodiversity changes occurring worldwide, we gathered data from 123 dryland ecosystems from six continents, including steppes, savannas, and shrublands (*SI Appendix, Fig. S1*), to investigate how multiple plant diversity attributes simultaneously influence multifunctionality. We used eight complementary biodiversity metrics that account for changes in the taxonomic, phylogenetic (early diverging and recent lineages), and functional diversity of plant communities (*Methods* and *SI Appendix, Fig. S2* and *Tables S1* and *S2*). Within this framework, our selection included metrics that were weighted and nonweighted by species abundance to disentangle the effect of dominant (mass ratio effects) vs. that of subordinate (richness effects) plant species on multifunctionality. After controlling for important climatic, soil, and geographic variables, we related multiple biodiversity metrics to four indices of multifunctionality using the multiple thresholds approach (30). The four indices were (i) multifunctionality (based on 11 weakly correlated functions), (ii) carbon cycling (C; including organic carbon concentration; pentose content and aboveground plant productivity), (iii) nitrogen cycling (N; including nitrate concentration, dissolved organic nitrogen, protein content, and potential nitrification), and (iv) phosphorus cycling (P; including available, inorganic and total phosphorus, and phosphatase enzymatic activity) (*SI Appendix, Table S3*). We tested the core hypothesis that considering multiple biodiversity attributes simultaneously increases the strength of biodiversity effects on multifunctionality.

## Results

The biodiversity metrics studied were strongly related to multifunctionality, even after accounting for the strong influence of geographic, climate, and soil properties on ecosystem functioning (Fig. 1). Biodiversity attributes explained up to 18% of multifunctionality (total variance) and up to 25, 22, and 27% of the variation in the indices derived for C, N, and P cycling, respectively. While species richness alone explained on average ~5% of variation in multifunctionality and up to 8% for C cycling, the inclusion of multiple biodiversity attributes enhanced the effect of biodiversity on multifunctionality by threefold. Functional, phylogenetic, and taxonomic biodiversity attributes were all selected in the most parsimonious models as significant predictors of multifunctionality, indicating that they have complementary effects on C, N, and P cycling.

Richness effects [the sum of explained variance of species richness and of nonweighted functional (FDIS) and phylogenetic (PSV and MNTD) metrics] explained between 76 and 100% of the biotic effects on multifunctionality (Fig. 2A). In contrast, the importance of dominant species through mass ratio effects (i.e., the metrics weighted by the abundance of the species) increased when considering each nutrient cycle individually (Fig. 2B–D). Mass ratio effects contributed, on average, to 51, 41, and 63% of the explained variance for C, N, and P cycling, respectively. Mass ratio effects were mostly related to the functional identity (CWM-SLA and CWM-H)

of dominant species rather than to their functional/phylogenetic diversities. In summary, richness effects due to subordinate species were the strongest predictors of multifunctionality, while mass ratio effects better explained C, N, and P cycling separately.

The net relationship between biodiversity and multifunctionality was generally positive, although weak, and even null when high multifunctionality thresholds were considered (Fig. 3A). This result was consistent regardless of the number of biodiversity attributes considered (Fig. 4) but varied with the nutrient studied. Thus, despite the larger amount of variance explained (Fig. 1), the net effect of biodiversity on ecosystem functioning was not stronger when multiple biodiversity attributes were included (Fig. 4). The inconsistency between variance explained and the net effect observed was mainly caused by contrasting effects of individual biodiversity attributes on different nutrient cycles taken separately and on overall multifunctionality.

When evaluating the sets of functions separately, we observed positive relationships between biodiversity and C and P cycling (Fig. 3B and D), which turned negative in the case of N cycling (Fig. 3C). In addition, we observed contrasting relationships depending on the biodiversity attribute considered (Fig. 5). Species richness and phylogenetic diversity (PSV) were positively related to multifunctionality (Fig. 5A) and to C, N, and P cycling (Fig. 5B–D). However, FDIS (describing the dispersion of functional trait values observed within communities) was negatively related to multifunctionality, C, and N cycling. These results highlight that particular combinations of biodiversity attributes are needed to maximize either targeted nutrient cycles or overall multifunctionality.

## Discussion

We investigated how multiple biodiversity attributes (taxonomic, phylogenetic, and functional richness and mass ratio effects) simultaneously influenced the multifunctionality of 123 drylands worldwide. Together, these attributes explained up to 27% of variation in multifunctionality across a wide range of geographic contexts, climatic, and soil conditions. The simultaneous effect of multiple biodiversity attributes on multifunctionality stresses the need to move from a single taxonomic to a more multidimensional perspective of biodiversity to better grasp its complex effects on the functioning of terrestrial ecosystems. The importance of considering multiple biodiversity attributes has been recently shown for biomass production and its temporal variability, or for N availability (9–11, 31). Our results expand this research by highlighting how multiple biodiversity attributes differentially impact both multifunctionality and major nutrient cycles at the global scale.

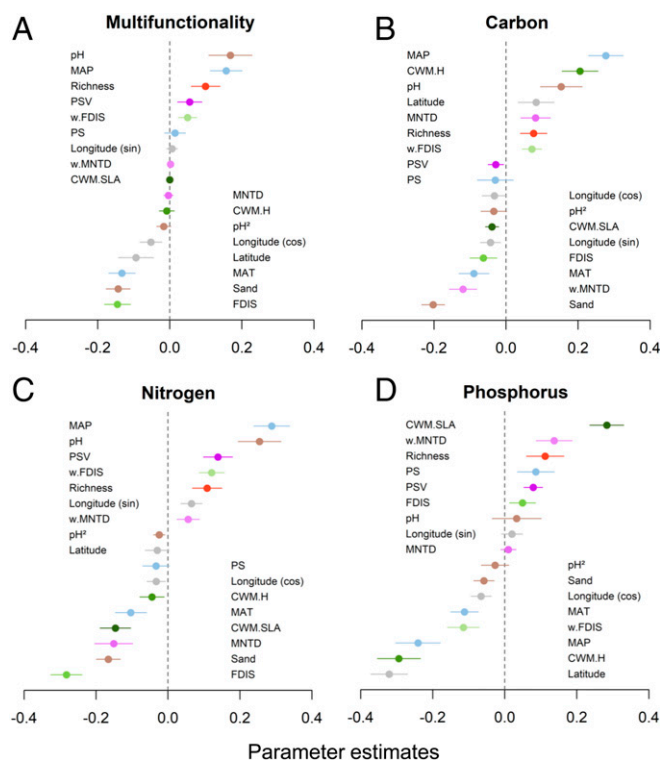
Our study helps to reconcile two influential hypotheses on the effects of biodiversity on ecosystem functioning (19, 25). Mass ratio effects (i.e., the abundance-weighted metrics considered, accounting for the effect of the most dominant species) were the strongest predictors related to individual nutrient cycles but were weakly correlated with multifunctionality. As such, the mass ratio hypothesis may not apply when considering multiple functions simultaneously (see also ref. 28). In contrast, richness effects (those mainly driven by subordinate species) were the almost exclusive biotic drivers of multifunctionality in the drylands studied. Our results show that richness effects increase in importance when aiming at maximizing multiple ecosystem functions simultaneously. This matches the common view that species are unique, i.e., that a high number of cooccurring subordinate species can promote different functions at different times and places, therefore maximizing the performance of multiple functions simultaneously (1, 2, 5, 6). Our study extends the view of taxonomic diversity to the phylogenetic and functional attributes of subordinate species as important predictors of multifunctionality in terrestrial ecosystems.

Biodiversity had an overall positive effect on multifunctionality when considering multiple biodiversity attributes simultaneously. However, and contrary to our hypothesis, this effect was relatively









**Fig. 5.** Standardized regression coefficients of model predictors and associated 95% confidence intervals for (A) multifunctionality and (B–D) C, N, and P cycling indices. Standardized regression coefficients result from model averaging procedures and are averaged across the entire spectrum of thresholds (20–80%) evaluated. Confidence intervals that do not cross the zero line indicate that the predictors under consideration are associated with a statistically significant ( $P < 0.05$ ) change in multifunctionality. See *SI Appendix, Table S4*, for the variation of standardized regression coefficients of each predictor along the threshold gradient evaluated.

cycles or overall multifunctionality, therefore optimizing the limited budgets allocated to maintain ecosystem functioning and associated services in drylands, the Earth's largest biome.

## Methods

**Characteristics of the Study Sites.** We obtained field data from 123 sites located in 13 countries (*SI Appendix, Fig. S1*). These sites (30 m × 30 m) are representative from the major vegetation types found in drylands and differ widely in plant species richness and environmental conditions (see further details in *SI Appendix, Fig. S1*).

**Ecosystem Multifunctionality.** We assessed ecosystem functioning at each site using 11 variables that provide a comprehensive and balanced design of C (organic C, pentose, plant productivity), N (nitrate, dissolved organic N, proteins, potential N transformation rate) and P (total and available P, activity of phosphatase and inorganic P) cycling and storage. These variables (hereafter functions) are uncorrelated with each other (see details in *SI Appendix, Table S3*), and together constitute a good proxy for nutrient cycling, biological productivity, and build-up of nutrient pools (3, 39–41).

We calculated four indices based either on all measured functions (multifunctionality) or on different set of functions representing C (three functions), N (four functions) and P (four functions) cycling (*SI Appendix, Table S3*). We standardized separately the 11 functions measured ( $F$ ) using the Z-score transformation:

$$Z\text{-score}_{ij} = \frac{F_{ij} - \text{Mean } F_i}{\text{SD } F_i}, \quad [1]$$

where  $F_{ij}$  is the value of a function  $i$  in the community  $j$ , and  $\text{Mean } F_i$  and  $\text{SD } F_i$  are the mean and the SD of the function  $F_i$  calculated for the 123 studied communities, respectively. We used a multiple threshold approach to evaluate whether multiple functions are simultaneously performing at high

levels (30). In short, this approach counts the number of functions that reach a given threshold (as the percent of the maximum value of each of the functions observed in the dataset). This maximum is taken as the top 5% values for each function observed across all study sites (42). Considering multiple thresholds allows a better understanding of how biodiversity affects ecosystem functioning and accounting for potential trade-offs between the functions evaluated (30). We considered thresholds between 20 and 80% (every 5%), since care should be taken to avoid overinterpreting results at very high or low thresholds (43). Each calculated threshold ( $T$ ) was smoothed by using a moving average with intervals  $[T - 10\%, T + 10\%]$ . We used this approach for all functions together and also for those that only relate to the C, N, and P cycling. We also calculated multifunctionality as the average of the standardized values across all functions (3, 15), obtaining results similar to those presented in the main text (*SI Appendix, Fig. S3*).

**Plant Diversity Attributes and Biodiversity Metrics.** Biodiversity effects on ecosystem functioning can arise from (i) dominant plant species through mass ratio effects (25) and (ii) subordinate species through richness effects (19). Both mass ratio and richness effects can encompass taxonomic, phylogenetic, and functional attributes (*SI Appendix, Fig. S2*). To account for all these possible biodiversity issues in our analyses (*SI Appendix, Table S2*). Studied metrics included taxonomic (species richness), functional [community-weighted mean for height and SLA (CWM.H and CWM.SLA) and weighted and nonweighted functional dispersion (w.FDIS and FDIS)] and phylogenetic [phylogenetic species variability (PSV) and weighted and nonweighted mean nearest taxon distance (w.MNTD and MNTD)] diversity (full methodological details in *SI Appendix, Figs. S2 and S4*).

The use of these metrics also allowed us to assess mass ratio (i.e., the functional identity and diversity of dominant species; sensu ref. 25) vs. richness effects by comparing abundance-weighted vs. nonweighted metrics. Considering MNTD and PSV allowed us to investigate whether ecosystem functioning relates to recent vs. early diverging evolutionary events, respectively (44). Finally, we must note that species evenness was not included in the present study due to its strong correlation with w.FDIS ( $r > 0.8$ , *SI Appendix, Table S1*).

**Environmental and Spatial Variables Considered.** Mean annual temperature (MAT), mean annual precipitation (MAP), and precipitation seasonality (PS; coefficient of variation of 12 monthly rainfall totals) were obtained from Worldclim ([www.worldclim.org](http://www.worldclim.org)), a high-resolution (30 arc s or ~1 km at equator) global database (45). These variables are major determinants of ecosystem structure and functioning in drylands worldwide (see ref. 46 for a review), were not highly correlated between them in our sites, and provide a comprehensive representation of climatic conditions.

We summarized local edaphic parameters at each site using soil sand content and pH. These variables, measured as described in Maestre et al. (3), play key roles in the availability of water and nutrients in drylands (47) and are major drivers of the composition and diversity of plant and microbial communities (41, 48). Clay and silt contents were not used in our analyses due to their correlation with sand content ( $r = -0.52$  and  $-0.55$ , respectively). By doing so we avoided overparameterizing our models and kept the number of environmental and biotic predictors of multifunctionality balanced in our analyses. We also considered the latitude and longitude of the study sites in our analyses to account for spatial autocorrelation in our data (3, 17, 31, 48) (see also *SI Appendix, Fig. S5*).

**Statistical Analyses.** Relationships between biodiversity attributes and the four indices of ecosystem functioning used were assessed using multiple linear regression models and sequentially repeated across multifunctionality thresholds ranging from 20 to 80%. The models included the following predictors: (i) geographic variables [latitude, longitude (sin) and longitude (cos)], abiotic variables (MAT, MAP, PS, soil sand content, and pH) and biodiversity metrics (species richness, CWM.SLA, CWM.H, FDIS, w.FDIS, PSV, MNTD, and w.MNTD). After inspecting the data, a quadratic term was allocated to soil pH to properly model nonlinear responses.

We used a model selection procedure for each threshold separately, based on minimizing the corrected Akaike information criterion (AICc), to select the best predictors of the four indices of ecosystem functioning. In a first step, we performed a model simplification using a backward regression procedure with the *stepAICc* function in *R*. We subsequently removed nonsignificant quadratic and interaction terms that did not impact the predictive ability of

the model. Then, a model selection procedure based on AICc selection ( $\Delta AICc < 2$ ) was applied on the resulting models to select the best predictors supported by the data. This procedure was performed using the *dredge* function in the R package *MuMIn* (49). Model residuals were inspected to ensure homoscedasticity and normality. All predictors and response variables were standardized before analyses using the Z-score to interpret parameter estimates on a comparable scale.

We evaluated the importance of the predictors under consideration as drivers of multifunctionality and sets of functions related to C, N, and P cycling. For doing so, we expressed the importance of predictors as the percentage of variance they explain, based on the comparison between the absolute values of their standardized regression coefficients and the sum of all standardized regression coefficients from all predictors in the models. This method is similar to a variance partition analysis because we previously transformed all predictors to Z-scores. The following identifiable variance fractions were then examined: (i) geography, (ii) climate, (iii) soil, and (iv) each of the different biodiversity metrics considered. We repeated this analysis to identify three variance fractions: the mass ratio effects through (i) the identity (CWM-H and CWM-SLA) and (ii) diversity of dominant species (w.FDIS and w.MNTD) and (iii) richness effects (all nonweighted metrics).

Net biodiversity effects were calculated as the sum of the standardized regression coefficients of all metrics of biodiversity selected during the model selection procedures. The data and supertree used in this paper are available in Figshare digital repository (50, 51).

**ACKNOWLEDGMENTS.** We thank all the members of the EPES-BIOCOM network for the collection of field data, as well as all the members of the F.T.M. laboratory for their help with data organization and management, and for their comments and suggestions on early stages of the manuscript. We are also grateful to the Editor, as well as two anonymous reviewers, for valuable comments on earlier versions. This work was funded by the European Research Council [ERC Grant Agreements 242658 (BIOCOM) and 647038 (BIO-DESERT)]. F.T.M., M.B., and Y.L.B.-P. are supported by the ERC (BIO-DESERT). Y.L.B.-P. was also supported by a Marie Skłodowska-Curie Actions Individual Fellowship within the European Program Horizon 2020 (DRYFUN Project 656035). S.S. was supported by the Spanish Government under a Ramón y Cajal Contract (RYC-2016-20604). N.G. was supported by the AgreeSkills+ fellowship programme, which has received funding from the European Union's Seventh Framework Programme under Grant Agreement FP7-609398 (AgreeSkills+ contract). This work was supported by the French government Initiatives d'Excellence-Initiatives Science/Innovation/Territoires/Économie (IDEX-ISITE) initiative 16-IDEX-0001 (CAP 20-25).

- Gamfeldt L, Hillebrand H, Jonsson PR (2008) Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223–1231.
- Isbell F, et al. (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202.
- Maestre FT, et al. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335:214–218.
- Soliveres S, et al. (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* 536:456–459.
- Meyer ST, et al. (2018) Biodiversity-multifunctionality relationships depend on identity and number of measured functions. *Nat Ecol Evol* 2:44–49.
- Gamfeldt L, Roger F (2017) Revisiting the biodiversity-ecosystem multifunctionality relationship. *Nat Ecol Evol* 1:168.
- Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and phylogenetic diversity as predictors of biodiversity—Ecosystem-function relationships. *Ecology* 92:1573–1581.
- Cadotte MW, Dinnage R, Tilman D (2012) Phylogenetic diversity promotes ecosystem stability. *Ecology* 93:223–233.
- Naeem S, et al. (2016) Biodiversity as a multidimensional construct: A review, framework and case study of herbivory's impact on plant biodiversity. *Proc Biol Sci* 283:20153005.
- Craven D, et al. (2018) Multiple facets of biodiversity drive the diversity-stability relationship. *Nat Ecol Evol* 2:1579–1587.
- Roger F, Bertilsson S, Langenheder S, Osman OA, Gamfeldt L (2016) Effects of multiple dimensions of bacterial diversity on functioning, stability and multifunctionality. *Ecology* 97:2716–2728.
- Brum FT, et al. (2017) Global priorities for conservation across multiple dimensions of mammalian diversity. *Proc Natl Acad Sci USA* 114:7641–7646.
- Tucker CM, Davies TJ, Cadotte MW, Pearse WD (2018) On the relationship between phylogenetic diversity and trait diversity. *Ecology* 99:1473–1479.
- Balvanera P, et al. (2014) Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *Bioscience* 64:49–57.
- Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One* 6:e17476.
- Valencia E, et al. (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytol* 206:660–671.
- Gross N, et al. (2017) Functional trait diversity maximizes ecosystem multifunctionality. *Nat Ecol Evol* 1:1–9.
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737.
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: Theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–1861.
- Cadotte MW, et al. (2017) Explaining ecosystem multifunction with evolutionary models. *Ecology* 98:3175–3187.
- Harmon LJ, et al. (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458:1167–1170.
- Venail P, et al. (2015) Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Funct Ecol* 29:615–626.
- Gilbert GS, Webb CO (2007) Phylogenetic signal in plant pathogen-host range. *Proc Natl Acad Sci USA* 104:4979–4983.
- Montesinos-Navarro A, Segarra-Moragues JG, Valiente-Banuet A, Verdú M (2015) Evidence for phylogenetic correlation of plant-AMF assemblages? *Ann Bot* 115:171–177.
- Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *J Ecol* 86:902–910.
- Garnier E, et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637.
- Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecol Lett* 6:509–517.
- Lyons KG, Brigham CA, Traut BH, Schwartz MW (2005) Rare species and ecosystem functioning. *Conserv Biol* 19:1019–1024.
- Soliveres S, et al. (2016) Locally rare species influence grassland ecosystem multifunctionality. Locally rare species influence grassland ecosystem multifunctionality. *Philos Trans R Soc B Biol Sci* 371:20150269.
- Byrnes JEK, et al. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods Ecol Evol* 5:111–124.
- García-Palacios P, Gross N, Gaitán J, Maestre FT (2018) Climate mediates the biodiversity-ecosystem stability relationship globally. *Proc Natl Acad Sci USA* 115:8400–8405.
- Cardinale BJ, et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos* 117:488–493.
- Ochoa-Hueso R, et al. (2018) Soil fungal abundance and plant functional traits drive fertile island formation in global drylands. *J Ecol* 106:242–253.
- Diaz S, et al. (2016) The global spectrum of plant form and function. *Nature* 529:167–171.
- Salguero-Gómez R, et al. (2015) The compadre plant matrix database: An open online repository for plant demography. *J Ecol* 103:202–218.
- Valiente-Banuet A, Verdú M (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecol Lett* 10:1029–1036.
- Cornwell WK, et al. (2014) Functional distinctiveness of major plant lineages. *J Ecol* 102:345–356.
- Whitford WG (2002) *Ecology of Desert Systems* (Academic, San Diego).
- Reynolds JF, et al. (2007) Global desertification: Building a science for dryland development. *Science* 316:847–851.
- Delgado-Baquerizo M, et al. (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat Commun* 7:10541.
- Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc Natl Acad Sci USA* 107:1443–1446.
- Lefcheck JS, et al. (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat Commun* 6:6936.
- Graham CH, Storch D, Machac A (2018) Phylogenetic scale in ecology and evolution. *Glob Ecol Biogeogr* 27:175–187.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol Int J Clim* 25:1965–1978.
- Maestre FT, Salguero-Gómez R, Quero JL (2012) It is getting hotter in here: Determining and projecting the impacts of global environmental change on drylands. *Philos Trans R Soc Lond B Biol Sci* 367:3062–3075.
- Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA. *Oecologia* 141:269–281.
- Le Bagousse-Pinguet Y, et al. (2017) Testing the environmental filtering concept in global drylands. *J Ecol* 105:1058–1069.
- Bartoń K (2017) MuMIn: Multi-model Inference. Version 1.40.0. Available at <https://CRAN.R-project.org/package=MuMIn>.
- Le Bagousse-Pinguet Y (2019) Dataset from “Phylogenetic, functional and taxonomic richness have both positive and negative effects on ecosystem multifunctionality.” Figshare. Available at [https://figshare.com/articles/Phylogenetic\\_functional\\_and\\_taxonomic\\_richness\\_have\\_both\\_positive\\_and\\_negative\\_effects\\_on\\_ecosystem\\_multifunctionality/7039799/1](https://figshare.com/articles/Phylogenetic_functional_and_taxonomic_richness_have_both_positive_and_negative_effects_on_ecosystem_multifunctionality/7039799/1). Deposited March 21, 2019.
- Le Bagousse-Pinguet Y, et al. (2019) Dataset from “2019\_PNAS\_Phylogenetic supertree.” Figshare. Available at [https://figshare.com/articles/Le\\_Bagousse-Pinguet\\_et\\_al\\_2019\\_PNAS\\_Phylogenetic\\_supertree/7594262/1](https://figshare.com/articles/Le_Bagousse-Pinguet_et_al_2019_PNAS_Phylogenetic_supertree/7594262/1). Deposited March 21, 2019.