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Soil fungal abundance and plant functional traits drive fertile island formation in global drylands

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F.T.M. designed the study and coordinated field data acquisition. S.S., D.J.E. and R.O.H. gathered trait data, with the assistance of all co-authors. M.D-B. conducted soil and molecular analyses. B.K.S. and T.J. provided the Illumina data and conducted bioinformatics analyses. All authors except R.O.H., B.K.S. and T.J. contributed field data. Data analyses were done by R.O.H. The paper was written by R.O.H., and all authors substantially contributed to the subsequent drafts.

Tweetable abstract

Fungi and plant traits drive fertile island formation in global drylands

SUMMARY

1. Dryland vegetation is characterised by discrete plant patches that accumulate and capture soil resources under their canopies. These "fertile islands" are major drivers of dryland ecosystem structure and functioning, yet we lack an integrated understanding of the factors controlling their magnitude and variability at the global scale.

2. We conducted a standardized field survey across two hundred and thirty-six drylands from five continents. At each site, we measured the composition, diversity and cover of perennial plants. Fertile island effects were estimated at each site by comparing composite soil samples obtained under the canopy of the dominant plants and in open areas devoid of perennial vegetation. For each sample, we measured fifteen soil variables (functions) associated with carbon, nitrogen and phosphorus cycling and used the Relative Interaction Index to quantify the magnitude of the fertile island effect for each function. In eighty sites, we also measured fungal and bacterial abundance (quantitative PCR) and diversity (Illumina MiSeq).

3. The most fertile islands, i.e. those where a higher number of functions were simultaneously enhanced, were found at lower-elevation sites with greater soil pH values and sand content under semiarid climates, particularly at locations where the presence of tall woody species with a low specific leaf area increased fungal abundance beneath plant canopies, the main direct biotic controller of the fertile island effect in the drylands studied. Positive effects of fungal abundance were particularly associated with greater nutrient contents and microbial activity (soil extracellular enzymes) under plant canopies.

4. *Synthesis.* Our results show that the formation of fertile islands in global drylands largely depends on: (i) local climatic, topographic and edaphic characteristics, (ii) the structure and traits of local plant communities and (iii) soil microbial communities. Our study also has broad implications for the management and restoration of dryland ecosystems worldwide, where woody plants are commonly used as nurse plants to enhance the establishment and survival of beneficiary species. Finally, our results suggest that forecasted increases in aridity may enhance the formation of fertile islands in drylands worldwide.

KEY-WORDS

Aridity; Drylands; Fertile islands; Fungal abundance; Multiple threshold approach; Plant functional traits; Relative interaction index; Soil properties

Introduction

Dryland ecosystems occupy about 45% of Earth’s land surface, store approximately 20% of the global soil carbon (C) pool, and contribute up to 30-35% of terrestrial net primary production (Millennium Ecosystem Assessment 2005; Huang *et al.* 2016; Prăvălie 2016). These ecosystems are characterised by discontinuous vegetation cover, with discrete vegetation patches dispersed within a matrix of bare soil, communities of annual plants and/or biological soil crusts (biocrusts, Eldridge 1999; Valentin *et al.* 1999). Dryland vegetation patches enhance dust capture, intercept water and nutrients from surface run-off after rainfall events, and have greater biological activity compared to adjacent areas, leading to the formation of the so-called fertile islands under them (Reynolds *et al.* 1999; Okin *et al.* 2004; de Graaff *et al.* 2014). These fertile islands have been described in drylands from all continents (e.g., Pausas *et al.* 2006; Butterfield & Briggs 2009; Allington & Valone 2014; Elliott *et al.* 2014), where they are a key determinant of ecosystem functioning (Whitford & Wade 2002). Factors such as soil texture, slope and rainfall patterns are known to determine the amount of run-off generated and, therefore, could plausibly account for the magnitude of the fertile island effect, defined as the relative difference between plant canopies and open areas devoid of vascular vegetation (Allington & Valone 2014). However, we do not know how ubiquitous the formation of fertile islands is globally, nor which are the main biotic and abiotic factors controlling their magnitude. Since dryland structure and function is inextricably tied to the fertile island phenomenon, a better understanding of these factors is essential to improve our ability to predict the ecological consequences of the climate change-induced expansion of drylands forecasted for the second half of this century (Huang *et al.* 2016).

Multiple properties of plant communities and individuals could also plausibly account for the degree of fertile island formation and their distribution among drylands. Plant community attributes such as total cover, relative woody plant cover and diversity, and plant functional traits such as height and specific leaf area (SLA, defined as the ratio of leaf area to dry mass), are frequently correlated with climatic conditions and soil properties as a consequence of a functional adaptation of plants to cope with their local environments (Jager *et al.* 2015; Le Bagousse-Pinguet *et al.* 2017). However, top-down effects of plant community attributes and functional traits on soil properties are also well documented as a consequence of variations in the quantity and quality of litter inputs (Cleveland *et al.* 2014; Valencia *et al.* 2015), differences in canopy shading (Breshears *et al.* 1997; Linstädter *et al.* 2016), and/or modifications in soil resource dynamics through nutrient redistribution and hydraulic lift (Prieto *et al.* 2011). Therefore, clear associations between community structure, functional traits of the focal plant (i.e., the plant under which the fertile island forms) and the properties of its associated fertile island are equally expected (Bonanomi, Incerti & Mazzoleni 2011). The efficiency in the capture of airborne particles and nutrients is also determined by canopy architecture, including the degree of contact with the ground and height (Coble & Hart 2013). Similarly, the ability to form symbiotic associations with rhizobacteria, and therefore to fix atmospheric N, as well as the functional type (herbs, shrubs and trees) have been documented as relevant traits in the formation of fertile islands (Bonanomi *et al.* 2011).

The abundance, diversity and composition of soil microbial communities largely control nutrient cycling and litter decomposition rates in drylands worldwide (Cleveland *et al.* 2014; Delgado-Baquerizo *et al.* 2016b). These attributes have been found to vary between vegetated and non-vegetated microsites in drylands, as they depend upon the quantity and quality of litter inputs and on the microclimatic conditions provided by plant patches (Elliott *et al.* 2014; Cleveland *et al.* 2014). For example, a greater abundance of both fungi and bacteria under plant canopies compared to adjacent open areas devoid of vascular vegetation is typically reported in drylands (Delgado-Baquerizo *et al.* 2013b; Elliott *et al.* 2014). Thus, the attributes of microbial communities could affect the ability of plant patches to capture and cycle nutrients, both directly (e.g., through nutrient fixation, litter decomposition and organic matter mineralization) and indirectly (e.g., through nutrient redistribution via fungal networks [Barto *et al.* 2011; Behie & Bidochka 2017]), enhancing the fertile island effect. Moreover, recent studies indicate that increasing aridity will reduce the diversity and abundance of soil fungal and bacterial communities in global drylands (Maestre *et al.* 2015), resulting in negative consequences for key ecosystem functions such as nutrient cycling and plant production (Delgado-Baquerizo *et al.* 2016). However, the implications of reductions in the abundance and diversity of soil microbes under increasing aridity scenarios for the formation of fertile islands remain largely unexplored.

In this study, we aimed at evaluating the role and the relative importance of plant and microbial community attributes, plant functional traits, and environmental variables on the magnitude of the fertile island effect in drylands worldwide. To do so, we used data from 236 dryland ecosystems from all continents except Antarctica (Supplementary Figure 1). We hypothesized that: (i) plant community attributes, such as plant diversity, total plant cover, and relative woody cover, (ii) plant functional traits, such as SLA and height, and (iii) soil microbial communities are the main direct drivers controlling the magnitude of the fertile island effect. In contrast, we predicted that climatic, topographic and edaphic conditions (aridity, altitude, slope, sand content and soil pH) exert a predominantly indirect role through their direct control on these biotic attributes. We specifically hypothesized that the fertile island effect is enhanced in dense, species-rich shrublands and woodlands dominated by woody species with low-SLA leaves (Valencia *et al.* 2015). These conditions are known to promote the deposition of greater amounts of less decomposable litter (Santiago 2007), which would result in greater organic matter accumulation rates. Greater amounts of less decomposable litter, together with greater soil pH, are known to enhance the presence of a well-developed network of fungal hyphae beneath focal plants, which is key to maximise nutrient cycling and sequestration rates (Collins *et al.* 2008). We also hypothesized that the presence of N fixers and plants with canopies touching the soil, thus favouring aeolian and water-transported sediment capture and retention, will increase the magnitude of the fertile island effect (Knops, Bradley & Wedin 2002; Coble & Hart 2013).

Material and methods

STUDY SITES

Soil samples were collected from 236 sites in 19 countries from five continents (Argentina, Australia, Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, USA and Venezuela). These sites include the 224 sites used in Maestre *et al.* (2012) plus 12 additional sites in Botswana, Ghana and Burkina Faso surveyed in 2012 and 2013 (Supplementary Figure 1). Sites were chosen to cover a wide spectrum of abiotic (climatic, soil type, slope) and biotic (type of vegetation, total cover, species richness) features characterizing drylands worldwide. In order to test for the consequences of increasing aridity levels (arid, semiarid and dry-subhumid) on the magnitude of fertile islands, we calculated the Aridity Index (AI, defined as precipitation/potential evapotranspiration) of each site as described in Zomer *et al.* (2008), who used data interpolation obtained from WorldClim (Hijmans *et al.* 2005). Since higher values of AI correspond with more mesic sites (less arid), we used 1-AI (hereafter 'aridity') as a surrogate of aridity to ease the interpretation of our results (Delgado-Baquerizo *et al.* 2013a).

VEGETATION SURVEY

All study sites were sampled following the same protocol. At each site, we surveyed 80 1.5 m × 1.5 m quadrats within one 30 m × 30 m plot. Quadrats were located along four 30-m long transects separated eight meters from each other. In each quadrat, we estimated the cover of all perennial plant species and used these data to estimate plant diversity (Shannon-Wiener index). In parallel, we calculated the relative coverage of woody plants along the transects using the line-intercept method (see Maestre *et al.* 2012 for methodological details).

SOIL COLLECTION, PLANT FUNCTIONAL TRAITS AND LABORATORY ANALYSES

Soils were sampled during the dry season using a stratified random procedure. At each plot, five 50 cm × 50 cm quadrats were randomly placed under the canopy of the dominant perennial vegetation patch type (i.e., tussock grasses, shrubs or trees, with one or two dominant patch types, depending on the site) and in open areas devoid of perennial vegetation (hence generating 10 or 15 soil samples per plot). A composite sample consisting of five soil cores (0-7.5 cm depth) was collected from each individual quadrat, bulked and homogenized in the field. Samples were subsequently bulked at the plot level separately for each microsite. This resulted in a composite sample for open areas per site, and one or two composite samples underneath plant patches, depending on the dominant plant patches (grass, shrub or tree) present. In 80 of the 236 sites surveyed, about 5 g of soil were stored at -20 °C after field collection for microbial analyses. These analyses were conducted on composite samples for each microsite (open and vegetated areas) and site, which resulted in 160 composite samples (see Maestre *et al.* 2015 for details). To avoid problems associated with the use of multiple laboratories when analysing soils from different sites, and to facilitate the comparison of results between them, dried and frozen soil samples from all locations were shipped to Spain for laboratory analyses.

We compiled a dataset of the functional traits of the dominant plant species beneath which soil samples had been collected from. These functional traits included: functional type (grass, shrub or tree), ability to fix atmospheric N (fixers vs. non-fixers), canopy in contact with the soil (a surrogate for canopy architecture, influencing, among others, the ability of plants to capture aeolian and water-transported sediments and their suitability for animal resting; yes, no), maximum height at maturity (hereafter referred to as height), and specific leaf area (SLA). We selected these traits because: (1) they are known to encapsulate plant form and functions globally (Díaz *et al.* 2016), (2) can be readily measured in the field or easily obtained from data available in the literature and, most importantly, (3) are known to influence soil fertility and nutrient cycling (Santiago 2007). We gathered *on site* trait data in some of our locations, but for most of them, data were obtained from literature searches (see Eldridge *et al.* [2011] and Supplementary Table 1 for detailed information on species-specific functional trait values and their source).

To quantify the fertile island effect, we measured fifteen relevant indicators of soil function (hereafter functions) associated with C, N and phosphorus (P) cycling (Maestre et al. 2012). These included: (1) organic C, pentoses, hexoses, phenols, aromatic compounds, and β-glucosidase activity for the C cycle; (2) total N, extractable nitrate and ammonium, amino acids, proteins, and potential N mineralization for the N cycle; and (3) total P, available (Olsen) P and phosphatase activity for the P cycle. These variables were measured as described in Maestre *et al.* (2012) and Delgado-Baquerizo *et al.* (2013a).

To test for the role of the abundance and diversity of microbial communities on the fertile island effect, DNA was extracted from 0.5 g of defrosted soil from the subset of sites for which frozen samples were available using the Powersoil® Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA). Quantitative PCR (qPCR) reactions were carried out in triplicate on an ABI 7300 Real-Time PCR (Applied Biosystems, Foster City, CA, USA). The bacterial 16S-rRNA genes and fungal internal transcribed spacer (ITS) were amplified with the Eub 338-Eub 518 and ITS 1-5.8S primer sets (Evans & Wallenstein 2012). Amplicons targeting the bacterial 16S rRNA and fungal ITS genes were sequenced using the Illumina Miseq platform (Caporaso *et al.* 2012) and the 341F/805R (bacteria) and FITS7/ITS4 (fungi) primer sets (Herlemann *et al.* 2011; Ihrmark *et al.* 2012) as described in Appendix A. Sequencing was done at the Next Generation Genome Sequencing Facility of the Western Sydney University (Australia). These data were used to calculate Shannon diversity indices for bacteria and fungi (see Maestre *et al.* 2015 for further details).

NUMERICAL AND STATISTICAL ANALYSES

We used the Relative Interaction index (RII; Armas, Ordiales & Pugnaire 2004) to estimate the magnitude of the fertile island effect for each function, defined as the relative difference between plant canopies and open areas devoid of vascular vegetation for each measured variable. The RII was calculated as:

$$RII = (Xc - Xo) / (Xc + Xo) \qquad \text{Eqn. (1)}$$

where X is the variable of interest and Xc and Xo are the values under the canopy and in open areas, respectively. This index ranges from -1 to 1, with RII values >0 representing situations in which values for soil fertility and functions are greater under plant canopies (i.e., there is a fertile island effect for a given variable). By using this index, we removed between-site variation in uncontrolled factors that could affect soil fertility in the sampled patches but that are not related to the magnitude of the fertile island effect.

We used a multiple threshold approach (Byrnes *et al.* 2014) to calculate an overall fertile island effect using fourteen soil biogeochemical variables (i.e., all variables measured except total soil P, for which we had missing values at some locations). This method assumes that a function is maximised when its value is above a given threshold (%) of functioning, based on the maximum value of that function across all sites, allowing to account for potential trade-offs in the effects of fertile islands for different functions. Thus, the fertile island effect can score integer values that range between zero and fourteen. Fertile islands are typically characterised for simultaneously enhancing several functions compared to the surrounding matrix of bare soil. Therefore, we assumed that the greater the number of functions that scored over a given threshold of functioning, the greater the magnitude of the fertile island effect at that given threshold is. The fertile island effects for thresholds between 5-99% of maximum functioning were calculated using the ´multifunc´ package (Byrnes *et al.* 2014) in R version 3.2.2 (R Core Team 2016). These calculations were done separately for each scale of analysis (i.e., sampling sites and focal plants) and for the subset of samples for which microbial data were available. In the latter analysis, and to account for the effect of differences in the abundance and diversity of microbial communities between vegetated and non-vegetated microsites, we calculated four additional RII values using the abundance and Shannon diversity of both bacteria and fungi.

After these calculations, we used general and generalised linear models (LMs and GLMs; ´lm´ and ´glm´ functions from the basic ´stats´ package) to evaluate the effects of aridity class (arid, semiarid and dry-subhumid) and categorical functional traits (growth form [grass, shrub, tree], N fixing ability, and canopy architecture [canopy touching the ground or not]) on individual soil functions (LMs) and on the overall fertile island effect for thresholds ranging between 10-90% in 10% increment intervals (GLMs with a Poisson distribution). We also evaluated the effect of these categorical traits on the fertile island effect based on the average value of thresholds between 10-90% (hereafter referred to as average fertile island effect). We then calculated the relationship between the fertile island effect at thresholds between 5-99% and plant and microbial community attributes, continuous plant functional traits (SLA and height), and edapho-climatic (aridity, sand and pH) and topographic (altitude, slope) variables (Poisson regression). Given that it has been recently suggested that the formation of fertile islands strongly depends on grazing pressure (Allington & Valone 2014), we also evaluated the relationship between the fertile island effect at thresholds between 5-99% and the percentage of land occupied by rangelands surrounding the study sites (data obtained from Ramankutty *et al.* [2010]). Due to the lack of a more direct measure of grazing pressure, we used this variable as our best surrogate for it. These analyses were done both at the scale relevant for each predictor variable, as already mentioned, and using the subset of sites for which all environmental drivers, plant community and individual plant-level data, and microbial variables were available (n = 68 sites; this number is slightly smaller than the number of microbial samples due to the absence of focal plant-level SLA data for some sites). In the very few cases in which a microbial sample corresponded to more than one focal plant, we averaged the SLA and height values of the species under which soil samples had been collected from.

To investigate the direct and indirect drivers of the magnitude of fertile islands, we selected one or two variables of each of the following categories (climate, soil properties, topography, plant functional traits and plant and microbial community attributes) to construct an *a priori* causal model that could be subsequently tested using structural equation modelling (SEM; Grace 2006). Due to sample size limitations, we sought a model with no more than ten independent variables plus the fertile island effect. We first screened the most informative predictors of the fertile island effect in each of the described categories. Predictor variables were selected based on their significant association with the fertile island effect in Figure 3 and Supplementary Figure 2. In cases when more than one indicator of topography, soil properties, plants or soil microbial communities appeared highly informative, we checked if these variables were weakly correlated (e.g., sand content and soil pH, SLA and height, relative woody cover and plant diversity, and fungal abundance and diversity), in which case they were both included in the model. We constructed an *a priori* model that contained four abiotic variables (aridity, altitude, sand content and soil pH) and six biotic attributes (relative woody cover, plant diversity, SLA, height, and fungal abundance and diversity). All relationships were modelled as linear relationships. Aridity and altitude were hypothesized to directly influence soil properties and all biotic attributes. Relationships between plant community attributes and functional traits were modelled as nondirectional, while they were considered to influence fungal abundance and diversity. Finally, all environmental variables and biotic attributes were predicted to directly affect the fertile island effect. Models were tested independently for the fertile island thresholds ranging between 10-90% in 10% increment intervals and for the average fertile island effect (see Results and Supplementary Table 2). In addition, given that there was a substantial amount of variance associated with each function not captured by our fertile island metric, we carried out separate models with all individual functions as focal dependent variables. All SEM analyses were done with the `lavaan` R package (Rosseel 2012).

Results

All evaluated functions and microbial abundances were consistently greater under plant canopies than in the open areas, as denoted by 95% confidence intervals of RII not overlapping zero (Figure 1 and Supplementary Figures 2-5). This was particularly evident for microbial abundance, enzymatic activities and recalcitrant C compounds (aromatics and phenols). In contrast, bacterial diversity was slightly smaller under plant canopies. The average fertile island effect was consistently greatest under semiarid climates, although arid climates also formed fertile islands at functioning thresholds between 40-80% (Figure 2a and Supplementary Figures 2-3). Fertile islands that simultaneously enhanced a higher number of functions were also associated with trees at all thresholds, whereas those fertile islands associated with shrubs and grasses were less pronounced (Fig. 2b and Supplementary Figure 3). The fertile island effect at thresholds between 70-90% was significantly enhanced by canopies not touching the ground (Fig. 2c, Supplementary Table 3 and Supplementary Figure 4). Total N and nitrate were the only functions that were significantly affected by canopy architecture (Supplementary Figure 4g,i). Nitrate availability was greater under plants with canopies in contact with the soil, while total N showed the opposite pattern. The magnitude of the fertile island effect was not related the ability of plants to fix N (Fig. 3d, Supplementary Table 3 and Supplementary Figure 5). However, N fixers showed greater amino acid concentration, but not available inorganic N, under their canopies (Supplementary Figure 5f, i).

At the site scale, the fertile island effect was positively related to aridity at thresholds between 27-90% (Fig. 3a), to plant cover at thresholds between 5-36% (Fig. 3c), to plant diversity at thresholds between 5-84% (Fig. 3d), and to relative woody cover at thresholds between 14-99% (Fig. 3e). Soil properties (sand content and pH) were associated with the fertile island effect at both high 58-88% and low 5-55% thresholds, respectively (Figure 3b,c). Altitude and slope were negatively associated with the fertile island effect at thresholds between 25-62% and 31-99%, respectively (Supplementary Figure 6), indicating that greater fertile island effects are found in flatter areas at lower-elevation sites. The percentage of land covered by rangelands (our surrogate of potential grazing pressure) was only weakly related to the fertile island effect at thresholds 68-69%, 73-75% and 78% (Supplementary Figure 7). At the focal plant scale, the fertile island effect was negatively related to SLA at thresholds between 11-42% (Fig. 3f) and positively to plant height at thresholds between 5-99% (Fig. 3g). Fungal abundance and diversity were positively and negatively related to the fertile island effect at thresholds between 30-99% and 45-99%, respectively (Fig. 3i,j). Bacterial diversity was weakly related to the fertile island effect at most thresholds between 61-99% (Fig. 3l).

Our analyses using the reduced set of sites for which all variables were available (n = 68) revealed that only a few of the abiotic and biotic attributes considered were still significantly related to the fertile island effect at any given threshold (Supplementary Figure 6). Aridity, altitude, slope, sand content and soil pH were related to the fertile island effect at thresholds between 39-99%, 20-94%, 40-99% and 12-81%, respectively, while relative woody cover, fungal abundance and diversity were also significantly related to the fertile island effect at thresholds between 20-99%, 9-99% and 39-99%, respectively (Fig. 3 and Supplementary Figure 6). In contrast, plant diversity and total cover, functional traits, and bacterial abundance were not significantly related to the fertile island effect at any threshold.

Our SEM explained 37% of the variance of the average fertile island effect (Fig. 4 and Supplementary Table 2). The percentage of variance explained for individual thresholds ranged between 29 and 41%, but all models were highly comparable to one another. The average model indicated that, in agreement with our previous analyses, greater sand content and soil pH at lower-elevation sites, the presence of taller plants and greater fungal abundance directly enhanced the fertile island effect in drylands worldwide, while fungal diversity had the opposite effect (Figs. 3 and 4, Supplementary Table 2 and 3, and Supplementary Figure 8). The effects of aridity were mostly indirect through its direct control on soil properties and plant height, while the predominantly indirect role of low SLA values was mediated by greater fungal abundance under plant canopies.

Models for separate functions consistently explained a lower proportion of the fertile island effect for each individual function than the most explicative model including all functions (models ranged between 17% [pentoses and ammonium] to 38% [pentoses]), although all models showed very good fit to our data, as indicated by low χ^2/degrees of freedom values (< 2) and non-significant χ^2 and RMSEA values (P > 0.1 in all cases; Supplementary Table 4). Considering all fifteen models reported in Supplementary Table 4, fungal abundance had a significant direct effect on the fertile island effect of nine functions, an effect that was particularly marked in the case of total nutrient contents and soil extracellular enzymes. Both functional traits (height and SLA) were direct positive drivers of the magnitude of the fertile island effect associated with aromatic compound accumulation. Plant diversity only contributed to the fertile island effect by increasing available nitrate under plant canopies, while greater relative woody cover enhanced the fertile island effect for hexoses, available P and proteins. Soil pH enhanced the magnitude of the fertile island effect for seven functions, while sand was a significantly direct driver only for total P. The combination of both direct and indirect effects of greater sand content enhanced the fertile island effect in the case of phenols.

Discussion

Our results indicate that the fertile island effect is a widespread phenomenon in drylands worldwide. They also provide novel evidence that the attributes of plant communities and individuals, together with the abundance and diversity of soil fungal communities, are important drivers of the formation of fertile islands in global drylands. This suggests that the fertile island effect is not only attributable to the activity of vascular plants (Reynolds *et al.* 1999), but should be extended to the microbial community present beneath the plant canopy. However, the abundance and diversity of soil microbial communities are known to be highly influenced by the amount and quality of plant litter inputs (Cleveland *et al.* 2014), implying an indirect plant trait control on the formation of fertile patches via microbial communities. The magnitude of the fertile island effect was greatest under trees and in arid and semiarid sites, as previously found by Pucheta *et al.* (2006) in Argentina. In addition, soils with relatively greater pH enhanced the fertile island effect for potential microbial degrading activity and recalcitrant carbon compound accumulation, supporting the tight control of pH on soil activity at global scales (Sinsabaugh *et al.* 2008) and also indicating the importance of soil properties for long-term C stabilization (Cotrufo *et al.* 2013).

Plant community attributes, particularly greater plant cover, could affect the magnitude of fertile islands through several mechanisms, including increasing nutrient redistribution efficiency (Schlesinger & Pilmanis 2010; Collins *et al.* 2014). Denser woody vegetation is likely to be associated with a more strongly developed root system that redistributes nutrients from the interspaces to the vegetated areas (Okin *et al.* 2015). Once acquired by the plant, these nutrients will recirculate more efficiently within the plant-soil system and will be released as litter/ rhizodeposits beneath the plant canopy before being decomposed and either immobilised by soil microbes or taken up by plant roots (Ridolfi, Laio & D'Odorico 2008). Areas with greater plant diversity may, in turn, promote the fertile island effect by harbouring more beneficial and active soil microbial communities (Van der Heijden *et al.* 2008; Schnitzer *et al.* 2011), which may also enhance ecosystem functioning by mobilising and re-translocating nutrients such as N more efficiently from the surrounding soil matrix (Van Der Heijden *et al.* 2008; Schnitzer *et al.* 2011; Graham *et al.* 2016). Greater plant cover and relative woody cover are also likely to provide a more suitable habitat for microbial communities than areas with sparser vegetation by buffering patch-level temperature extremes and maintaining greater soil moisture values, thus resulting in greater soil fertility (Cortina & Maestre 2005).

Our study also provides empirical support for the notion that plant traits are major drivers of fertile island formation. Taller species with relatively low SLA values were those that most enhanced the fertile island effect, in agreement with a recent study (Valencia *et al.* 2015), although these effects were mostly indirect via fungal communities, particularly in the case of SLA. Possible mechanisms include the fact that taller trees tend to provide better branches for birds to perch (Pausas *et al.* 2006), better shading for animals (including livestock) due to a higher canopy density and larger canopy area (Linstädter *et al.* 2016), and a better capture of aeolian particles and a promotion of hydraulic lift (Okin *et al.* 2004). Taller woody plants also usually account for a higher biomass per individual, and hence produce more litter. These litter inputs will accumulate and, depending on their properties, decompose at different rates. High-SLA leaves are likely to be decomposed and/or consumed quickly, leaving little behind to contribute to the stable carbon pool (Diaz *et al.* 2004). However, low-SLA litter will remain under the plant canopy for longer periods of time, and will most likely be incorporated into the stable organic matter pool. This process would be favoured by a more active and abundant fungal community, as supported by our SEM. In contrast, the direct effects of SLA appeared to be consistently positive, particularly for C-degrading extracellular enzymes and aromatic compounds, suggesting that, in agreement with the recent literature (Cotrufo *et al.* 2015), labile C sources can be equally stabilised in the long-term organic matter pool. The direct and indirect effects of SLA on the fertile island effect cancelled each other out in our SEMs, supporting the lack of relationship between SLA and the fertile island effect at any given threshold in the reduced dataset. However, the negative association between SLA and the fertile island effect for thresholds between 11-42% when the analysis was carried out using the complete dataset suggests that the indirect negative effects of greater SLA through fungal abundance might be more important than the direct positive effects. The fact that we did not detect a clear link between the ability of nurse plants to fix N and the magnitude of their associated fertile island, as calculated with the multiple threshold approach, is surprising, as most studies assume a significant association between the ability of plants to symbiotically fix N and the formation of fertile islands (Bonanomi *et al.* 2011). However, we observed greater concentration of amino acids under the canopy of N fixers, and also a clear trend toward higher ammonium availability, a result consistent with what has been reported previously (Bonanomi *et al.* 2011).

The formation of fertile islands has also been recently attributed to the effects of grazing (Allington & Valone 2014), a major driver of ecosystem change in drylands worldwide (Asner *et al.* 2004). In our study, we did not directly account for differences in grazing pressure, but evaluated the potential association of fertile islands with the proportion of land covered by rangelands, an indirect measure of potential grazing pressure. In contrast to this hypothesis, we found no clear evidence of an association between the proportion of land occupied by rangelands and the fertile island effect. However, we did show that the magnitude of the fertile island effect can be attributed to differences in plant cover, woody cover, plant functional traits and fungal abundance and diversity, all attributes that have previously been shown to be influenced by grazing (Asner *et al.* 2004; Díaz *et al.* 2007). This leaves this question unresolved and, thus, open to be answered by a more targeted global survey accounting for the effects of grazing on fertile island formation.

CONCLUDING REMARKS

Our study provides new evidence suggesting that the formation of fertile islands in global drylands largely depends on attributes of the local plant and microbial communities and on environmental variables such as aridity, altitude and soil properties. Specifically, we have shown that the fertile island effect is enhanced in lower-elevation dense arid and semiarid shrublands and woodlands, where sand content and pH are greater and where vegetation is dominated by tall woody plants with leaves having low SLA values. These conditions are likely favouring the development of active and complex fungal communities under plant canopies, which our data suggest as one of the main direct drivers of fertile island formation. A more developed network of hyphal connections among scattered plants may result in a more efficient processing and redistribution of soil resources found in the interspaces, which are then remobilised towards the vegetated areas, further contributing to the creation of a mosaic landscape (Collins *et al.* 2008). Our study also has broad implications for the management and restoration of dryland ecosystems worldwide, where woody plants are commonly used as nurse plants to enhance the establishment and survival of beneficiary species (Cortina & Maestre 2005). For example, selection of adequate native woody, tall species based on their lower SLA values and inoculation with native, drought-resistant fungal strains could help to maximise restoration success rates by enhancing the formation of fertile islands. Finally, this study also helps us understand potential feedbacks between climate change and dryland ecosystems, as forecasted widespread increases in aridity will likely increase the formation of fertile islands worldwide.

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DATA ACCESIBILITY

Data used in this study can be obtained from https://figshare.com/s/c0a34c8541383b332172 (doi: 10.6084/m9.figshare.4710364).

REFERENCES

Allington, G.R.H. & Valone, T.J. (2014) Islands of fertility: A byproduct of grazing? *Ecosystems*, **17**, 127–141.

Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: A new comparative index. *Ecology*, **85(10)**, 2682–2686.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. & Harris, A.T. (2004) Grazing systems, ecosystem responses and global change. *Annual Review of Environmental Resources*, **29**, 261–299.

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F.T., Maire, V., de Bello, F., Fonseca, C.R., Kattge, J., Valencia, E., Leps, J. & Liancourt, P. (2017) Testing the environmental filtering concept in global drylands. *Journal of Ecology*, n/a-n/a.

Barto, E.K., Hilker, M., Müller, F., Mohney, B.K., Weidenhamer, J.D. & Rillig, M.C. (2011) The Fungal Fast Lane: Common Mycorrhizal Networks Extend Bioactive Zones of Allelochemicals in Soils. *PLOS ONE*, **6**, e27195.

Behie, S.W. & Bidochka, M.J. (2017) Nutrient transfer in plant–fungal symbioses. *Trends in Plant Science*, **19**, 734–740.

Bonanomi, G., Incerti, G. & Mazzoleni, S. (2011) Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems. *Plant Ecology*, **212**, 1777–1790.

Breshears, D.D., Rich, P.M., Barnes, F.J., Campbell, K., Applications, E., Nov, N. & Bell, E. (1997) Overstory-imposed heterogeneity in solar Radiation and Soil Moisture in a Semiarid Woodland. *Ecological Applications*, **7**, 1201–1215.

Butterfield, B.J. & Briggs, J.M. (2009) Patch dynamics of soil biotic feedbacks in the Sonoran Desert. *Journal of Arid Environments*, **73**, 96–102.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B.J., Hooper, D.U., Dee, L.E. & Duffy, J.E. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, **5**, 111–124.

Caporaso, J.G., Lauber, C.L., Walters, W. a, Berg-Lyons, D., Huntley, J., Fierer, N., Owens, S.M., Betley, J., Fraser, L., Bauer, M., Gormley, N., Gilbert, J. a, Smith, G. & Knight, R. (2012) Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *The ISME Journal*, **6**, 1621–1624.

Cleveland, C.C., Reed, S.C., Keller, A.B., Nemergut, D.R., O'Neill, S.P., Ostertag, R. & Vitousek, P.M. (2014) Litter quality versus soil microbial community controls over decomposition: A quantitative analysis. *Oecologia*, **174**, 283–94.

Coble, A.A. & Hart, S.C. (2013) The significance of atmospheric nutrient inputs and canopy interception of precipitation during ecosystem development in piñon–juniper woodlands of the southwestern USA. *Journal of Arid Environments*, **98**, 79–87.

Collins, S.L., Belnap, J., Grimm, N.B., Rudgers, J.A., Dahm, C.N., D'Odorico, P., Litvak, M., Natvig, D.O., Peters, D.C., Pockman, W.T., Sinsabaugh, R.L. & Wolf, B.O. (2014) A multiscale, hierarchical model of pulse dynamics in arid-land ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 397–419.

Collins, S.L., Sinsabaugh, R.L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M. & Zeglin, L.H. (2008) Pulse dynamics and microbial processes in aridland ecosystems. *Journal of Ecology*, **96**, 413–420.

Cortina, J. & Maestre, F.T. (2005) Plant effects on soils in drylands: Implications for community dynamics and ecosystem restoration. *Tree species effects on soils: Implications for global change* (eds D. Binkley & O. Menyailo), pp. 85–118. NATO Science Series, Kluwer Academic Publishers, Dordrecht.

Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H. & Parton, W.J.

(2015) Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, **8**, 776–779.

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K. & Paul, E. (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology*, **19**, 988–995.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M. a, Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S., García-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T., Barraza-Zepeda, C., Bran, D., Carreira, J.A., Chaieb, M., Conceição, A.A., Derak, M., Eldridge, D.J., Escudero, A., Espinosa, C.I., Gaitán, J., Gatica, M.G., Gómez-González, S., Guzman, E., Gutiérrez, J.R., Florentino, A., Hepper, E., Hernández, R.M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R.L., Miriti, M., Monerris, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramírez, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres, D., Torres-Díaz, C., Ungar, E.D., Val, J., Wamiti, W., Wang, D. & Zaady, E. (2013a) Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, **502**, 672–6.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Quero, J.L., Ochoa, V., García-Gómez, M., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Noumi, Z., Derak, M. & Wallenstein, M.D. (2013b) Aridity modulates N availability in arid and semiarid Mediterranean grasslands. *PloS one*, **8**, e59807.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D. & Singh, B.K. (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nature Communications*, **7**, 10541.

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, a, Montserrat-Marti, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M.C., Shirvany, F. a, Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, a, Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, a, Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, a, Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Christopher, B., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–171.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B.D. (2007) Plant trait responses to grazing - A global synthesis. *Global Change Biology*, **13**, 313–341.

Eldridge, D.J. (1999) Distribution and floristics of moss- and lichen-dominated soil crusts in a patterned *Callitris glaucophylla* woodland in eastern Australia. *Acta Oecologica*, **20**, 159–170.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecology Letters*, **14**, 709–722.

Elliott, D.R., Thomas, A.D., Hoon, S.R. & Sen, R. (2014) Niche partitioning of bacterial communities in biological crusts and soils under grasses, shrubs and trees in the Kalahari. *Biodiversity and Conservation*, **23**, 1709–1733.

Evans, S.E. & Wallenstein, M.D. (2012) Soil microbial community response to drying and rewetting stress: Does historical precipitation regime matter? *Biogeochemistry*, **109**, 101–116.

de Graaff, M.-A., Throop, H.L., Verburg, P.S.J., Arnone, J.A. & Campos, X. (2014) A synthesis of climate and vegetation cover effects on biogeochemical cycling in shrub-dominated drylands. *Ecosystems*, **17**, 931–945.

Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge.

Graham, E.B., Knelman, J.E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A., Beman, J.M., Abell, G., Philippot, L., Prosser, J., Foulquier, A., Yuste, J.C., Glanville, H.C., Jones, D.L., Angel, R., Salminen, J., Newton, R.J., Bürgmann, H., Ingram, L.J., Hamer, U., Siljanen, H.M.P., Peltoniemi, K., Potthast, K., Bañeras, L., Hartmann, M., Banerjee, S., Yu, R.-Q., Nogaro, G., Richter, A., Koranda, M., Castle, S.C., Goberna, M., Song, B., Chatterjee, A., Nunes, O.C., Lopes, A.R., Cao, Y., Kaisermann, A., Hallin, S., Strickland, M.S., Garcia-Pausas, J., Barba, J., Kang, H., Isobe, K., Papaspyrou, S., Pastorelli, R., Lagomarsino, A., Lindström, E.S., Basiliko, N. & Nemergut, D.R. (2016) Microbes as engines of ecosystem function: When does community structure enhance predictions of ecosystem processes? *Frontiers in Microbiology*, **7**, 1–10.

Van Der Heijden, M.G.A., Bardgett, R.D. & Van Straalen, N.M. (2008) The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, **11**, 296–310.

Herlemann, D.P., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J.J. & Andersson, A.F. (2011) Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal*, **5**, 1571–1579.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Huang, J., Yu, H., Guan, X., Wang, G. & Guo, R. (2016) Accelerated dryland expansion under climate change. *Nature Climate Change*, **6**, 166–172.

Ihrmark, K., Bödeker, I.T.M.M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K.E. & Lindahl, B.D. (2012) New primers to amplify the fungal ITS2 region - Evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology*, **82**, 666–677.

Jager, M.M., Richardson, S.J., Bellingham, P.J., Clearwater, M.J. & Laughlin, D.C. (2015) Soil fertility induces coordinated responses of multiple independent functional traits (ed G De Deyn). *Journal of Ecology*, **103**, 374–385.

Knops, J.M.H., Bradley, K.L. & Wedin, D.A. (2002) Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*, **5**, 454–466.

Linstädter, A., Bora, Z., Tolera, A. & Angassa, A. (2016) Are trees of intermediate density more facilitative? Canopy effects of four East African legume trees. *Applied Vegetation Science*, **19**, 291–303.

Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J. & Ochoa, V. (2015) Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Science, USA*, **112**, 15684–15689.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitan, J., Gatica, M.G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J.R., Hernandez, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D.A., Romao, R., Tighe, M., Torres-Diaz, C., Val, J., Veiga, J.P., Wang, D. & Zaady, E. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science*, **335**, 214–218.

Millennium Ecosystem Assessment. (2005) *Ecosystems and Human Well-Being: Biodiversity*

Synthesis.

Okin, G.S., Heras, M.M. Las, Saco, P.M., Throop, H.L., Vivoni, E.R., Parsons, A.J., Wainwright, J. & Peters, D.P. (2015) Connectivity in dryland landscapes: Shifting concepts of spatial interactions. *Frontiers in Ecology and the Environment*, **13**, 20–27.

Okin, G.S., Mahowald, N., Chadwick, O.A. & Artaxo, P. (2004) Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. *Global Biogeochemical Cycles*, **18**, doi: 10.1029/2003GB002145.

Pausas, J.G., Bonet, A., Maestre, F.T. & Climent, A. (2006) The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecologica*, **29**, 346–352.

Prăvălie, R. (2016) Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, **161**, 259–278.

Prieto, I., Padilla, F.M., Armas, C. & Pugnaire, F.I. (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 181–187.

Pucheta, E., Lllanos, M., Meglioli, C., Gaviorno, M., Ruiz, M. & Parera, C. (2006) Litter decomposition in a sandy Monte desert of western Argentina: Influences of vegetation patches and summer rainfall. *Austral Ecology*, **31**, 808–816.

R Core Team. (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramankutty, N., Evan, A.T., Monfreda, C. & Foley, J.A. (2010) *Global Agricultural Lands: Croplands, 2000*. Data distributed by the Socioeconomic Data and Applications Center (SEDAC).

Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G. & Tremmel, D.C. (1999) Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development.

Ecological Monographs, **69**, 69–106.

Ridolfi, L., Laio, F. & D'Odorico, P. (2008) Fertility island formation and evolution in dryland ecosystems. *Ecology and Society*, **13**, 5.

Rosseel, Y. (2012) lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software*, **41**, 1–36.

Santiago, L.S. (2007) Extending the leaf economics spectrum to decomposition: Evidence from a tropical forest. *Ecology*, **88**, 1126–1131.

Schlesinger, W.H. & Pilmanis, A.M. (2010) Plant-soil interactions in deserts. *Biogeochemistry*, **42**, 169–187.

Schnitzer, S.A., Klironomos, J.N., HilleRisLambers, J., Kinkel, L.L., Reich, P.B., Xiao, K., Rillig, M.C., Sikes, B.A., Callaway, R.M., Mangan, S.A., Van Nes, E.H. & Scheffer, M. (2011) Soil microbes drive the classic plant diversity-productivity pattern. *Ecology*, **92**, 296–303.

Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R. & Zeglin, L.H. (2008) Stoichiometry of soil enzyme activity at global scale. *Ecology letters*, **11**, 1252–64.

Valencia, E., Maestre, F.T., Bagousse-pinguet, Y. Le, Quero, L., Tamme, R., Le Bagousse-Pinguet, Y., Quero, J.L., Tamme, R., Borger, L., Garcia-Gomez, M. & Gross, N. (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*, **206**, 660–671.

Valentin, C., D'Herbès, J.M. & Poesen, J. (1999) Soil and water components of banded vegetation patterns. *Catena*, **37**, 1–24.

Whitford, W. & Wade, E.L. (2002) *Ecology of Desert Systems*. Elsevier.

Zomer, R.J., Trabucco, A., Bossio, D.A. & Verchot, L. V. (2008) Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems and Environment*, **126**, 67–80.

Figure legends

Figure 1. Effects of plant canopies on soil fertility, as measured with the Relative Interaction Index (RII, Eqn. 1), for 15 soil functions related to the C (blue bars), N (green bars) and P (red bars) cycles, and microbial community attributes (fungal and bacterial abundance and diversity; yellow bars). N min = nitrogen mineralization. Bact/Fungal abund = bacterial/fungal abundance. Bact/fungal H' = bacterial/fungal Shannon diversity. Bars are means ± 95% confidence intervals; confidence intervals not crossing the zero line indicate a significant fertile island effect. RII values higher than 0 indicate a positive fertile island effect (i.e., higher values of the function of interest under plant canopies compared to the bare interspaces).

Figure 2. Effect of plant canopies on soil fertility, calculated as the average of thresholds between 10-90% of maximum functioning, depending on: (a) aridity class (n = 226), (b) plant functional type (n = 322), (c) canopy architecture (n = 326), and (d) the ability of the focal plant to fix atmospheric N (n = 326). The effect of aridity class was analysed at the site level, while the effects of functional traits were analysed at the focal plant level. Different lowercase letters indicate significant ($P < 0.05$) differences between groups (Tukey test). Bars are means ± 1SE.

Figure 3. Slope of the relationship between the fertile island effect at thresholds between 5-99% and selected biotic and abiotic drivers: (a) aridity (n = 226), (b) altitude (n = 226), (c) slope (n = 226), (d) sand (n = 226), (e) pH (n = 226), (f) cover (n = 226), (g) plant diversity (n = 226), (h) relative woody cover (RWC) (n = 226), (i) specific leaf area (SLA) (n = 240), (j) plant maximum height (n = 326), (k) fungal abundance (n = 80), (l) fungal diversity (n = 79). No overlap between the 95% confidence interval and the zero line for a given threshold indicates a significant association between the fertile island effect at that threshold and the variable of interest. T_{min} and T_{max} indicate the minimum and maximum thresholds at which the relationship between the fertile island effect and the predictor variable of interest are

significantly related, respectively, while T_{me} indicates the threshold at which the slope of that relationship is steepest within the T_{min}-T_{max} interval.

Figure 4. Structural equation model showing the direct and indirect effects of abiotic and biotic drivers on the magnitude of fertile island formation (n = 68). The fertile island effect was calculated for the average fertile island effect (see Material and Methods). Solid black lines represent positive, linear associations, while dashed lines indicate negative, linear associations. The width of the arrows is proportional to the strength of the relationship (Supplementary Table 2). Non-significant direct effects tested in the model are shown in grey (for a greater detail of explanation, see Material and Methods). $^{**}P < 0.01$, $^{*}P < 0.05$. Square boxes indicate simple variables, although biotic factors have been grouped to ease visual interpretation. Nondirectional associations between plant community attributes and functional traits are not depicted to ease visualization.

Figure 1

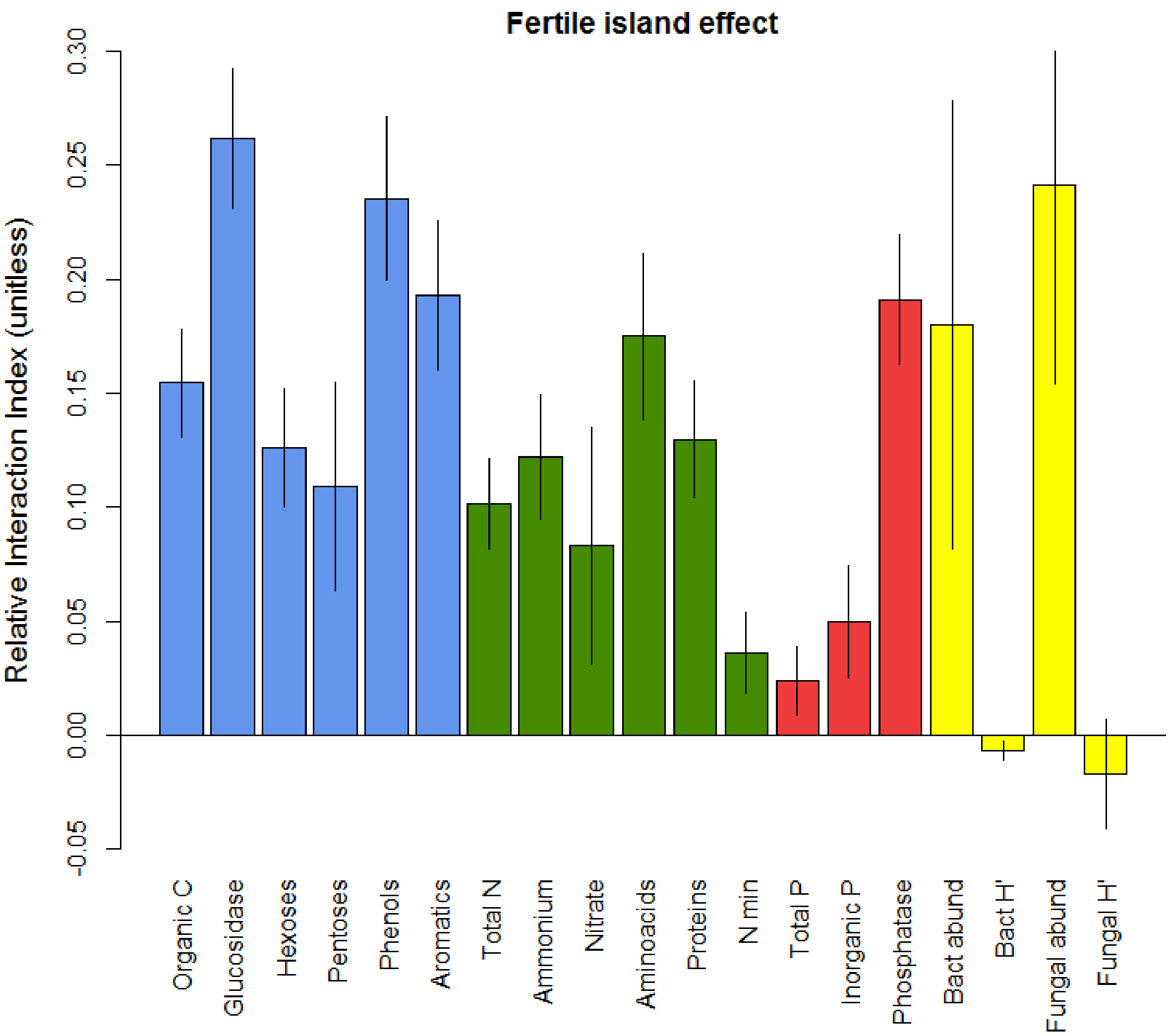
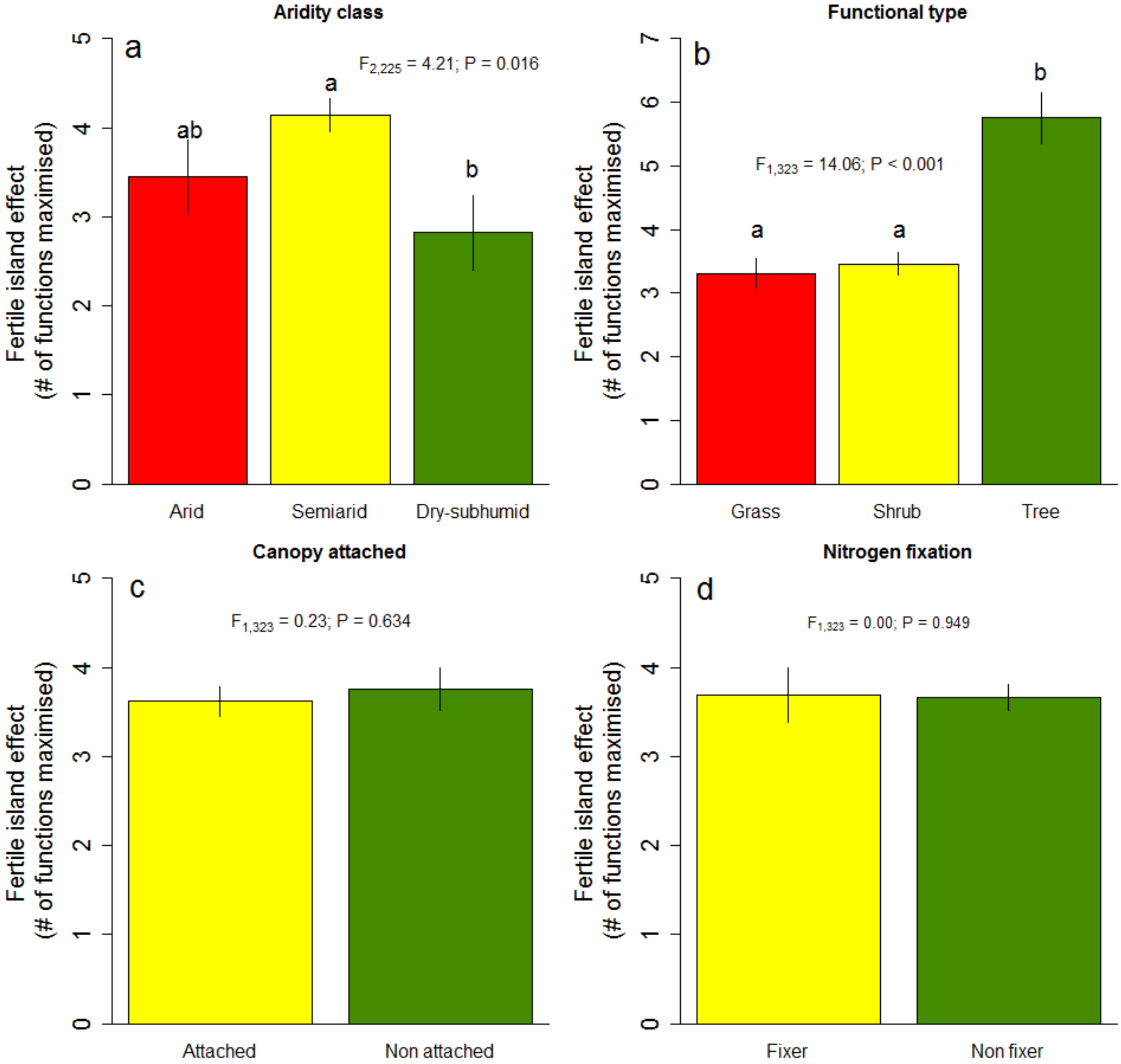
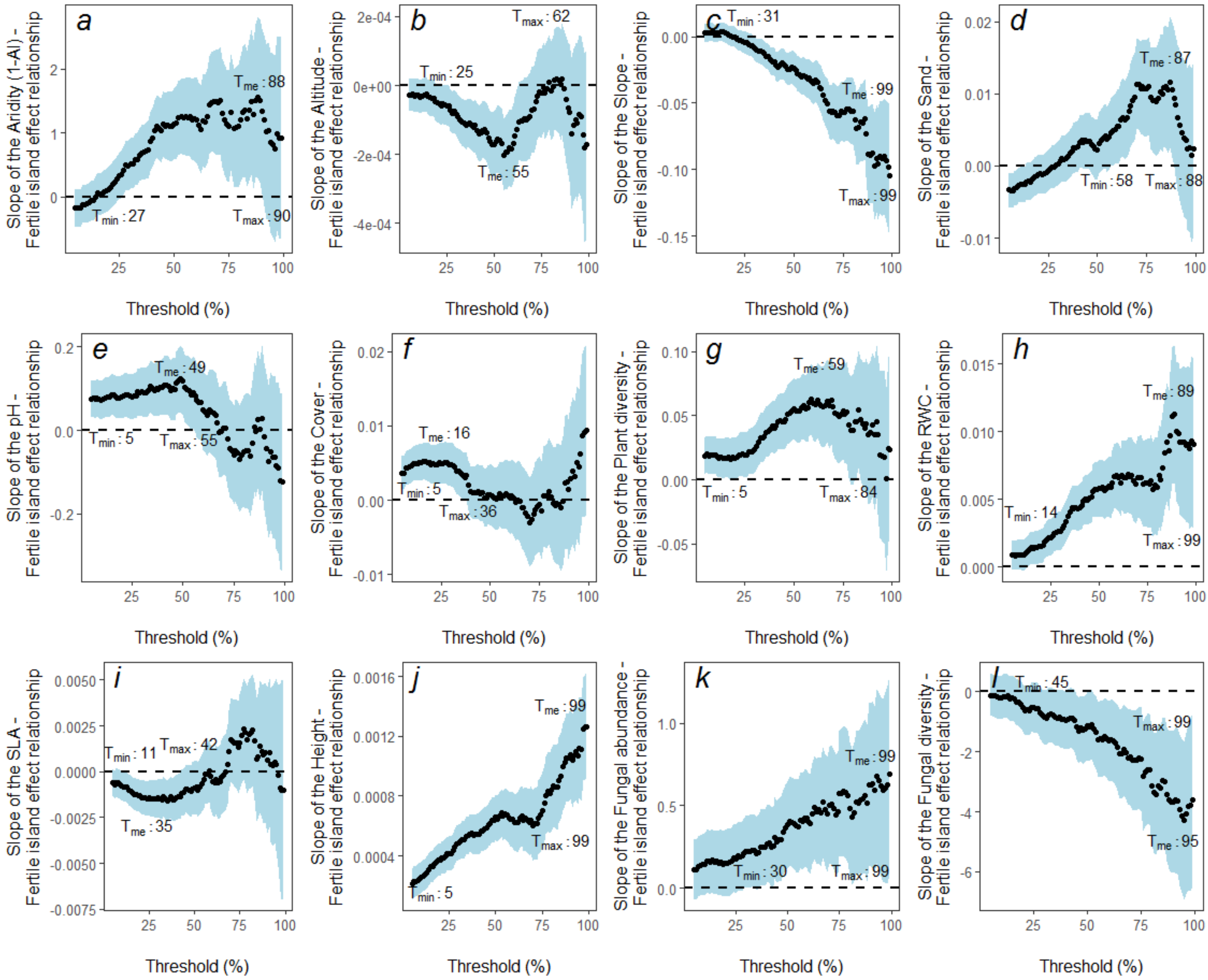

Fertile island effect
Relative Interaction Index (unitless)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
Organic C
Glucosidase
Hexoses
Pentoses
Phenols
Aromatics
Total N
Ammonium
Nitrate
Aminoacids
Proteins
N min
Total P
Inorganic P
Phosphatase
Bact abund
Bact H'
Fungal abund
Fungal H'

Figure 2



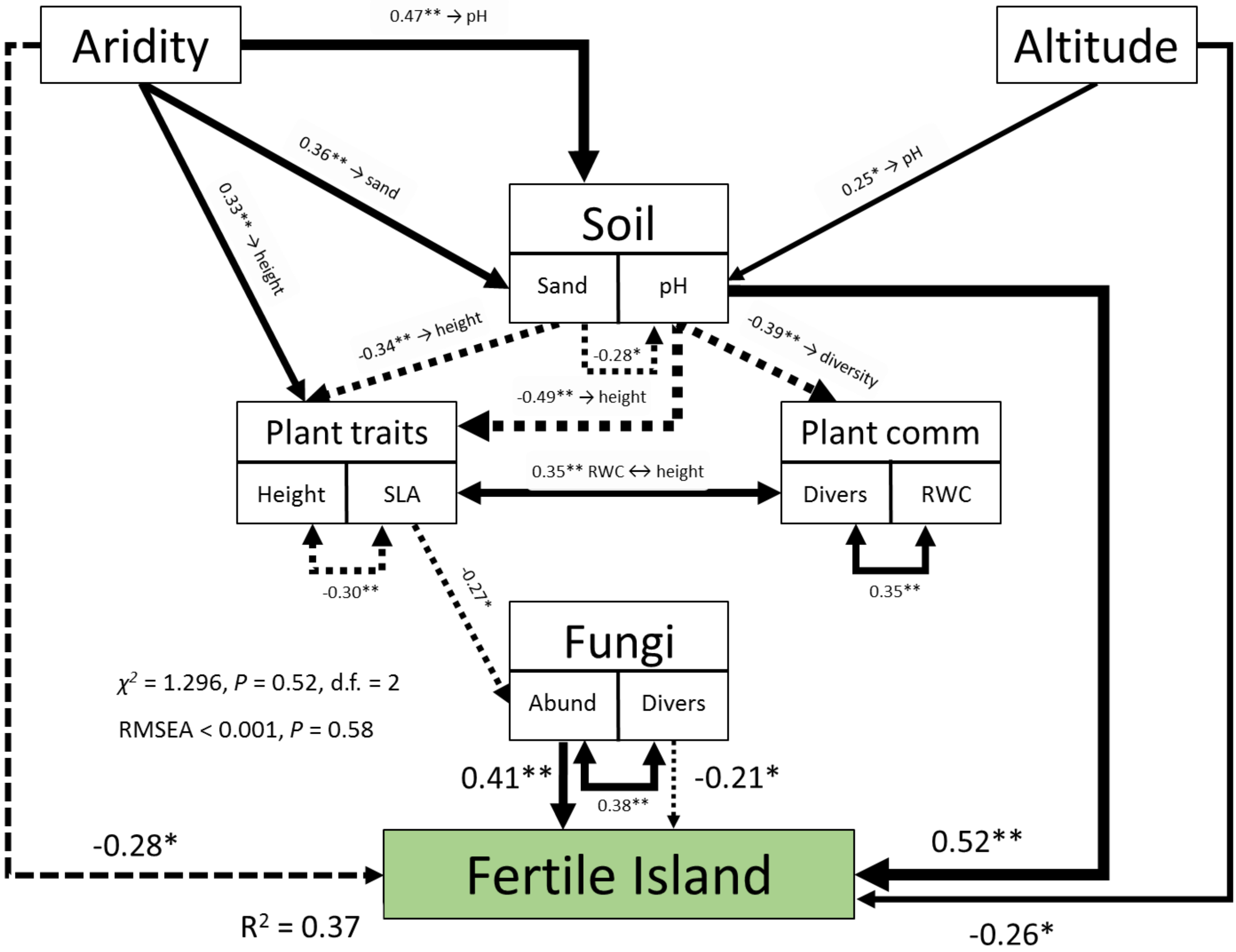
Aridity class
a
F2,225 = 4.21; P = 0.016
ab
a
b
Fertile island effect
(# of functions maximised)
Arid
Semiarid
Dry-subhumid
Functional type
b
F1,323 = 14.06; P < 0.001
a
a
b
Grass
Shrub
Tree
Canopy attached
c
F1,323 = 0.23; P = 0.634
Attached
Non attached
Nitrogen fixation
d
F1,323 = 0.00; P = 0.949
Fixer
Non fixer

Figure 3



a
Slope of the Aridity (1-AI) - Fertile island effect relationship
T_me : 88
T_min : 27
T_max : 90
b
Slope of the Altitude - Fertile island effect relationship
T_max : 62
T_min : 25
T_me : 55
c
Slope of the Slope - Fertile island effect relationship
T_min : 31
T_me : 99
T_max : 99
d
Slope of the Sand - Fertile island effect relationship
T_me : 87
T_min : 58
T_max : 88
e
Slope of the pH - Fertile island effect relationship
T_me : 49
T_min : 5
T_max : 55
f
Slope of the Cover - Fertile island effect relationship
T_me : 16
T_min : 5
T_max : 36
g
Slope of the Plant diversity - Fertile island effect relationship
T_me : 59
T_min : 5
T_max : 84
h
Slope of the RWC - Fertile island effect relationship
T_me : 89
T_min : 14
T_max : 99
i
Slope of the SLA - Fertile island effect relationship
T_min : 11
T_max : 42
T_me : 35
j
Slope of the Height - Fertile island effect relationship
T_me : 99
T_max : 99
T_min : 5
k
Slope of the Fungal abundance - Fertile island effect relationship
T_me : 99
T_min : 30
T_max : 99
l
Slope of the Fungal diversity - Fertile island effect relationship
T_min : 45
T_max : 99
T_me : 95
Threshold (%)

Figure 4



Aridity
0.47** → pH
Altitude
0.36** → sand
0.33** → height
0.25* → pH
Soil
Sand
pH
-0.34** → height
-0.28*
-0.39** → diversity
-0.49** → height
Plant traits
Height
SLA
0.35** RWC ↔ height
Plant comm
Divers
RWC
-0.30**
-0.27*
0.35**
Fungi
Abund
Divers
χ² = 1.296, P = 0.52, d.f. = 2
RMSEA < 0.001, P = 0.58
0.41**
0.38**
-0.21*
-0.28*
0.52**
Fertile Island
R² = 0.37
-0.26*