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Aridity Decouples C:N:P Stoichiometry Across Multiple Trophic Levels in Terrestrial Ecosystems

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Abstract

Increases in aridity forecasted by the end of this century will decouple the cycles of soil carbon (C), nitrogen (N) and phosphorus (P) in drylands—the largest terrestrial biome on Earth. Little is known, however, about how changes in aridity simultaneously affect the C:N:P stoichiometry of organisms across multiple trophic levels. It is imperative that we understand how aridity affects ecological stoichiometry so that we can develop strategies to mitigate any effects of changing climates. We characterized the C, N, P concentration and stoichiometry of soils, autotrophs (trees, N-fixing shrubs, grasses and mosses) and heterotrophs (microbes and ants) across a wide aridity gradient in Australia. Our results suggest that increases in aridity by the end of this century may alter the C:N:P stoichiometry of heterotrophs (ants and microbes), non-woody plants and in soil, but will not affect that one from woody plants. In particular, increases in aridity were positively related to C:P and N:P ratios in microbes and ants, negatively related to concentration of C, and the C:N and C:P ratios in mosses and/or short grasses, and not related to the C:N:P stoichiometry of either shrubs or trees. Because of the predominant role of C:N:P stoichiometry in driving nutrient cycling, our findings provide useful contextual information to determine ecological responses in a drier world.

Key words: carbon; nitrogen; phosphorus; heterotrophs; autotrophs; soil microbes; ants.

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Introduction

There is increasing evidence that projected increases of aridity by the end of this century (Feng and Fu 2013; Huang and others 2016) will alter soil carbon (C), nitrogen (N) and phosphorus (P) cycles in terrestrial ecosystems (Delgado-Baquerizo and others 2013; Wang and others 2014; Yuan and Chen 2015; Rabbi and others 2015; Jiao and others 2016). In particular, aridity is expected to reduce the concentrations of biologically controlled elements such as C and N in soils, as well as the soil C:P and N:P ratios (Fig. 1). This expectation is based on the fact that aridity reduces the positive effect of biotic components such as plants on C and N (for example, via reductions in plant cover), but increases concentrations of total P, which is primarily derived from rock weathering (Fig. 1; Delgado-Baquerizo and others 2013). By impacting both biologically and abiotically controlled elements in opposite ways, increasing aridity will potentially decouple (that is, push in opposite directions) the cycles of soil C and N versus P. Though the impact of aridity on soil C:N:P stoichiometry has been documented previously (Delgado-Baquerizo and others 2013; Wang and others 2014; Yuan and Chen 2015; Jiao and others 2016), the simultaneous impacts of increased aridity conditions on the nutrient concentrations and stoichiometric relationships in above- and belowground biota are largely unknown.

Nutrient availability and stoichiometry play critical roles in regulating ecosystem functions and services, such as nutrient cycling, habitat variability, litter decomposition and food production and quality (Elser and others 2000; Sardans and others 2012; Zechmeister-Boltenstern and others 2015). Thus, understanding the effects of increasing aridity on the nutrient economy and stoichiometry of biotic components is necessary to adequately predict changes in ecosystem functions and services in a more arid world. Assessing the impacts of aridity on stoichiometric relationships is particularly important for drylands, as they cover 45% of Earth's land surface (Prăvălie 2016), and their extent is predicted to increase by 11–23% by the end of this century (Huang and others 2016). However, despite the importance of ecological stoichiometry for ecosystem functioning (see Zechmeister-Boltenstern and others 2015 for a review), little is known about whether the responses of C, N and P concentration and stoichiometry in aboveground and belowground biota mirror those previously reported in dryland soils (Delgado-Baquerizo and others 2013; He and others 2015; Jiao and others 2016). Furthermore, no previous study has, to our knowledge, evaluated the simultaneous responses of multiple trophic levels to predicted increases in aridity such as those forecasted with global change. Thus, the effects of aridity on the C:N:P stoichiometry of multiple trophic levels, including plants, insects and microbes, are uncertain.

To advance our understanding of this important issue, we characterized the C, N, P concentration and stoichiometry of soils, autotrophs (trees, N-fixing shrubs, grasses and biocrust-forming mosses) and heterotrophs (microbes and ants) across a wide aridity gradient in eastern Australia. We tested the hypothesis that the response of C:N:P stoichiometry of plants to increases in aridity will be different from that of insects and microbes (Fig. 1). In par-

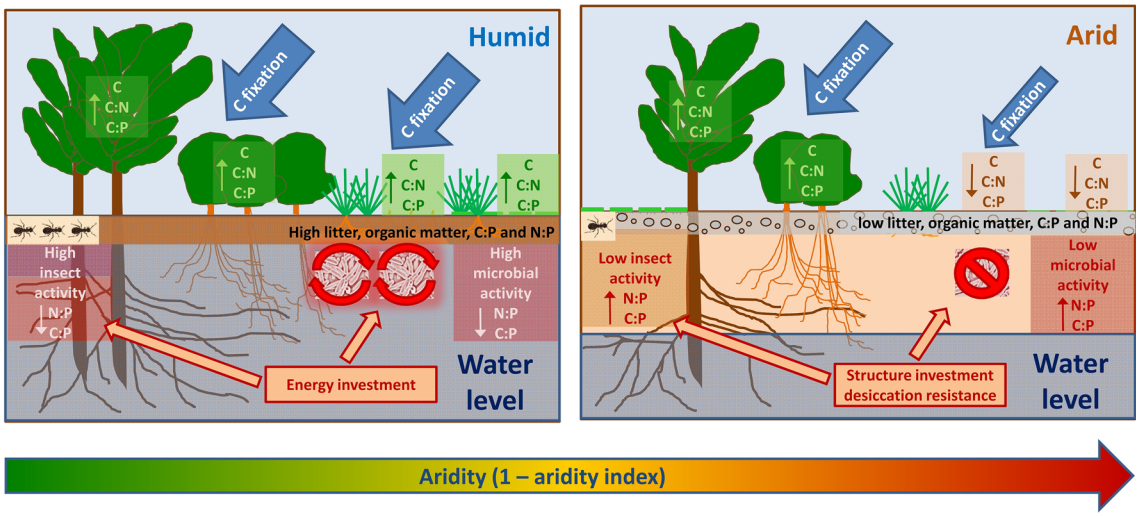

Figure 1. Conceptual framework exploring how ecological stoichiometry responds to increases in aridity for soil, autotrophic and heterotrophic organisms.

ticular, we expect increases in C:P and N:P ratios in microbes and ants, and reductions in the concentration of C, and the C:N and C:P ratios in mosses and/or short grasses with increases in aridity. The main reasons supporting the divergent response of the C:N:P stoichiometry of plants and soil organisms to increases in aridity include: (1) differential capacity to obtain water: perennial plants in general, and woody plants in particular, are less reliant on surface water than insects (for example, ants) and near-surface microbes, as their root systems allow them to access water from deeper soil layers, making them more resistant to increases in aridity; (2) use of organic C: unlike heterotrophs, plants mainly obtain C from the atmosphere (but see Näsholm and others 1998) via photosynthesis. Thus, reductions in photosynthetic rates linked to water stress may result in low C concentration and C:N and C:P ratios; and (3) fast-growing rates: insects and soil microbes have rapid growth rates (compared with perennial plants) and are more mobile. Both require considerable energy, and hence, they have a high P demand (Peñuelas and Sardans 2009). Consequently, the tissues from heterotrophic organisms are often relatively richer in P and have lower C concentration and C:P and N:P ratios than those in perennial plants (Cease and others 2012; Cease and Elser 2013; Zechmeister-Boltenstern and others 2015; Carnicer and others 2015). More specifically, increasing water availability is known to enhance biological activity in drylands (Whitford 1978; Frenette-Dussault and others 2013). Humid environments may promote life strategies based on optimizing energy, which is required to support a growth energy-demanding lifestyle. This requires comparatively high levels of N and P to sustain production rates of P- and N-rich organelles and molecules such as ribosomes, ATP, DNA and RNA. Thus, heterotrophic organisms may need to switch from a strategy of high-energy investment (high P, N and low C:P and N:P ratios; Fig. 1) to one that prioritizes investing in structure (low P, N and high C:P and N:P ratios; Fig. 1; Reich 2014). This change in strategy responds to the reduced capacity to obtain water and to tolerate increasing aridity under the most arid conditions of heterotrophs compared to autotrophs. In fact, increases in aridity, which reduce microbial and insect abundance and activity (Whitford 1978; Frenette-Dussault and others 2013; Delgado-Baquerizo and others 2013; Maestre and others 2015), may favor a strategy based on optimizing structure moving from a ''resource-acquisitive'' versus ''resource-conservative'' strategy (sensu Chapin 1980 and Reich 2014). To survive in more arid environments, these organisms will produce structures that promote desiccation tolerance, such as cell walls, structural proteins, fatty acids and waxy molecules; all of them were mainly based on C or N chemistry leading to increases in tissue C:P and N:P ratios (Csonka 1989; Schimel and others 2007). In addition, the C:N:P stoichiometry of all autotrophic communities is not expected to response in the same manner to increases in aridity, with non-woody plants being more affected than woody plants as a consequence of their lower capacity to obtain water and survive water stress. See Appendix S1 for additional rationale regarding the expected differing responses of woody versus non-woody plant species to increases in aridity (Fig. 1).

Methods

Study Area and Sampling

This study was carried out at 22 *Eucalyptus* forests from eastern Australia (Fig. S1). Locations for this study were chosen to represent a wide range of aridity conditions (from arid to humid ecosystems). Aridity Index (precipitation/potential evapotranspiration), total annual precipitation and mean temperature ranged from 0.19 to 0.80, 280 to 1167 mm and from 12.8 to 17.5°C, respectively. Note that temperature was related neither to precipitation (Spearman's $\rho = -0.121$; $P = 0.592$; $n = 22$) nor to Aridity Index (Spearman's $\rho = -0.123$; $P = 0.587$; $n = 22$) across the sites studied. The underlying geology across these sites varied from Ordovician sedimentary material in the east to Quaternary Pleistocene alluvium and colluvium on the western plains. Despite the different geological substrates, the soils derived from these materials show marked similarities, with generally gradational profiles and clay loam to loamy surface textures. We surveyed areas of similar aspect, generally southerly, and slope (<2%) to minimize the influence of factors other than climate in our conclusions. Perennial vegetation cover ranged from 18 to 98%. Locations in this study were selected to always use the same genus/species of plants, mosses or ants: *Eucalyptus* spp., *Acacia* spp., C3 native grass *Rhytidosperma* spp., biocrust-forming mosses (*Barbula calycina*, *Campylopus* spp. and *Didymodon torquatus*) and soil-foraging ants (*Iridomyrmex purpureus*) (see Table S1 for a list of the species sampled at each plot).

Sampling was carried out in March 2014 (end of the dry season). At each site, we established a 30 m × 30 m plot. Aridity was determined as 1-Aridity Index [AI], where AI = precipitation/po-

tential evapotranspiration (UNEP 1992). We obtained values of the Aridity Index (AI, precipitation/potential evapotranspiration) at 1 km resolution from Zomer and others (2008). At each site, three soil cores (0–5 cm depth) were collected in open areas (bare ground without mosses or any other visible biocrust component) between vegetation patches. Note that, in drylands, nutrient availability and microbial activity mainly take place in the first few centimeters of soils (Pointing and Belnap 2012). We focused on bare ground areas because microclimatic amelioration by plant canopies may confound the effects of aridity on soil stoichiometry. Soil cores were then mixed to obtain a composite soil sample for each microsite and site. A microsite is defined as a microenvironment given by particular biotic (for example, identify of plant species and functional groups) and abiotic features (for example, bare ground areas) within a particular location (that is, at the local scale). After field sampling, the soil was sieved (2-mm mesh). Soil was air-dried indoor (~35% humidity and ~25°C) for one month before physicochemical analyses. Previous studies have found that air-drying and further storage of dryland soils do not appreciably alter variables such as those we studied (Zornoza and others 2006, 2009). Thus, the potential bias induced by our drying treatment is expected to be minimal, as soils were already dry when we collected them. Additionally, in most sites, we were able to collect leaf samples from grasses (n = 21), N-fixing shrubs (n = 21) and trees (n = 22), thalli from mosses (n = 20) and ants (n = 16). See Table S1 for a list of the species sampled at each plot. In all cases, a composite sample from ten individuals was collected per plot. Ants were directly collected from visible ant nests. Tissue material was dried in the oven (70°C) and ground before chemical analyses. In the case of soil mosses, we used an air compressor to remove any visible soil particle from the moss thalli to reduce soil contamination as much as possible. Moreover, we would like to highlight that the digestion procedures used here (explained below) to characterize P mainly focus on the organic fractions—rather than on the mineral fractions, which are more abundant in soil. In this respect, any effect of soil contamination on the chemistry of soil mosses should have been fairly small.

C:N:P Measurements

We measured the concentration of C, N and P in soils, non-woody short vascular (grasses) and non-vascular plants (mosses), woody tall vascular plants (N-fixing shrubs and trees), soil microbes and ants. For soils, we measured both total and available (that is, soil solution pools) C, N and P concentrations and mass ratios. Soil available nutrients are readily available for plants and microbes, but have high temporal (hours to days) and spatial variability. Total nutrients represent a pool of nutrients that is much less variable, but is available for plants and microbes in the longer term (years to centuries). The concentration of total organic C in soil, plants, mosses and ants was determined as described in Anderson and Ingram (1993). Total N in these samples was measured with a CN analyzer (LECO CHN628 Series, LECO Corporation, St Joseph, MI, USA); total P was obtained using a SKALAR San++ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulfuric acid (3 h at 415°C) as described in Anderson and Ingram (1993). The concentration of total available C (dissolved organic C) and N (sum of organic and inorganic N) was measured from these extracts using a TOC/TON analyzer (TOC–Vcsh, Shimadzu, Kyoto, Japan) after 0.5 M K_2SO_4 extraction as described in Jones and Willett (2006). Olsen inorganic P was measured following a 0.5 M $NaHCO_3$ (pH 8.5) extraction (Olsen and others 1954) and determined colorimetrically (Tiessen and Moir 1993). Microbial biomass C, N and P was determined using the fumigation-extraction method as explained in Voroney and others (2006). Soil nutrient and microbial concentration were expressed on an oven-dry basis.

Statistical Analyses

We used a non-metric multidimensional ordination (NMDS) to explore overall variability in multidimensional C, N and P concentration and ratios across the above- and belowground components evaluated. These analyses allow us to visualize overall differences in the concentrations and ratios of C, N and P across different belowground (soil total, available and microbes) and aboveground (biocrust mosses, grasses, N-fixing shrubs, trees and ants) components at a glance. The two-dimensional NMDS solution provided a suitable representation of the data (stress = 0.08; excellent to good stress according to Clarke 1993). Prior to these analyses, data were standardized (z-transformed) and $\log_{10}$-transformed to avoid overrepresentation of particular variables in these analyses. We conducted NMDS analyses using Euclidean distance with the PRIMER v6 statistical package for Windows (PRIMER-E Ltd., Plymouth Marine Laboratory, UK). We also calculated the correlations (Spearman's ρ)

Table 1. Mean Values (±SE) of Carbon, Nitrogen and Phosphorus Concentration and Ratios in Soil Total and Available (n = 22), Microbes (n = 19), Grasses (Leaf; n = 21), N-Fixing Shrubs (Leaf; n = 21), Trees (Leaf; n = 22), Mosses (Thalli; n = 20) and Ants (Body; n = 16) Along the Studied Aridity Gradient

	Soil			Autotrophs			Heterotrophs	
	Soil total	Soil available	Biocrust mosses	Grasses	N-fixing shrubs	Trees	Ants	Microbes
C (%)	2.22 (0.32)	1.59×10^{-2} (1.52×10^{-3})	17.04 (1.76)	44.05 (1.16)	55.52 (1.01)	53.88 (0.78)	47.76 (4.54)	1.59×10^{-2} (3.70×10^{-3})
N (%)	0.14 (0.02)	2.21×10^{-3} (2.50×10^{-4})	0.59 (0.08)	1.43 (0.14)	2.07 (0.13)	1.22 (0.09)	7.56 (0.87)	3.08×10^{-3} (6.70×10^{-4})
P (%)	0.02 (0.00)	2.10×10^{-4} (4.00×10^{-5})	0.05 (0.01)	0.08 (0.01)	0.08 (0.01)	0.07 (0.01)	0.43 (0.06)	6.30×10^{-4} (1.60×10^{-4})
C:P	119.70 (18.65)	184.84 (53.46)	440.71 (74.61)	722.15 (110.31)	860.17 (99.89)	872.67 (72.39)	125.35 (13.65)	34.28 (6.38)
N:P	6.88 (0.66)	24.70 (7.10)	12.53 (1.34)	18.64 (1.07)	28.10 (1.84)	17.92 (0.98)	19.04 (2.23)	7.03 (1.07)
C:N	16.61 (1.44)	7.41 (0.35)	36.32 (6.44)	37.54 (4.05)	29.99 (2.92)	48.86 (3.68)	6.86 (0.45)	5.80 (1.01)

Soil nutrient and microbial concentration were expressed on an oven-dry basis.

between the axes of this NMDS with the concentrations and ratios of C, N and P to identify the variables driving changes along these axes.

Most importantly, to test our hypotheses (Fig. 1) we calculated the correlations (Spearman's ρ) between aridity (1-Aridity Index) and C, N and P concentration and ratios for the different belowground and aboveground components evaluated. We used rank-based correlation Spearman's ρ because this metric is robust to deviations from normality and is largely used in the ecological literature (see Nakagawa and Cuthill 2007 for a review). To further test whether Spearman's ρ differed significantly from zero, we assessed whether bias-corrected 95% bootstrap confidence intervals of Spearman's ρ did not overlap zero based on 9999 iterations (Rosenberg and others 2000; see García-Palacios and others 2013 for a similar approach). Bias-corrected 95% bootstrap confidence intervals are a much more conservative method than P values calculated from Spearman rank correlations, explaining slightly differences between the significant levels provided for these two methods.

Finally, we tested for overall differences between Aridity classes: arid (Aridity Index < 0.50 − arid and semiarid) versus humid (Aridity Index > 0.50 − dry subhumid and humid) ecosystems for C, N and P concentration and ratios across belowground (soil total, soil available and soil microbes) and aboveground components (biocrust mosses, grasses, N-fixing shrubs, trees, ants and microbes) using a one-way ANOVA with aridity class as a fixed factor.

Results

As expected, autotrophs (mosses, grasses, N-fixing shrubs and trees) had the highest mass C:P ratios, while soils, ants and microbes had the lowest C:P ratio. Soil available and microbial C, N and P comprised less than 5% of the total soil C, N and P concentrations. In general, trees and N-fixing shrubs had the highest C concentration (Table 1). Ants, N-fixing shrubs and grasses had the highest total concentrations of N and P, and soil available (that is, nutrient pools) and microbes had the lowest concentration of C, N and P along the aridity gradient studied (Table 1). N-fixing shrubs and microbes/soil (total) showed the highest and lowest N:P ratios, respectively, and trees/shrubs and microbes/ants had the highest and the lowest C:N ratios, respectively. Ordination analyses separated organisms into two groups: (1) autotrophs (mosses, grasses, N-fixing shrubs and trees) and (2) soil/soil organisms (Fig. 2; Table S2).

Aridity showed an overall negative correlation with total and available soil C, mosses and grasses (Fig. 3), but did not correlate with C concentration in N-fixing shrubs, trees, microbes or ants (Fig. 3). Aridity was negatively and positively correlated with N in soil available and ant tissues, respectively, and positively and negatively correlated with the concentration of P in microbes and soil (available), respectively. Similar results were found when we explored the impacts of different aridity classes on C, N and P concentration and stoichiometry (Figs. S2 and S3). Aridity was negatively

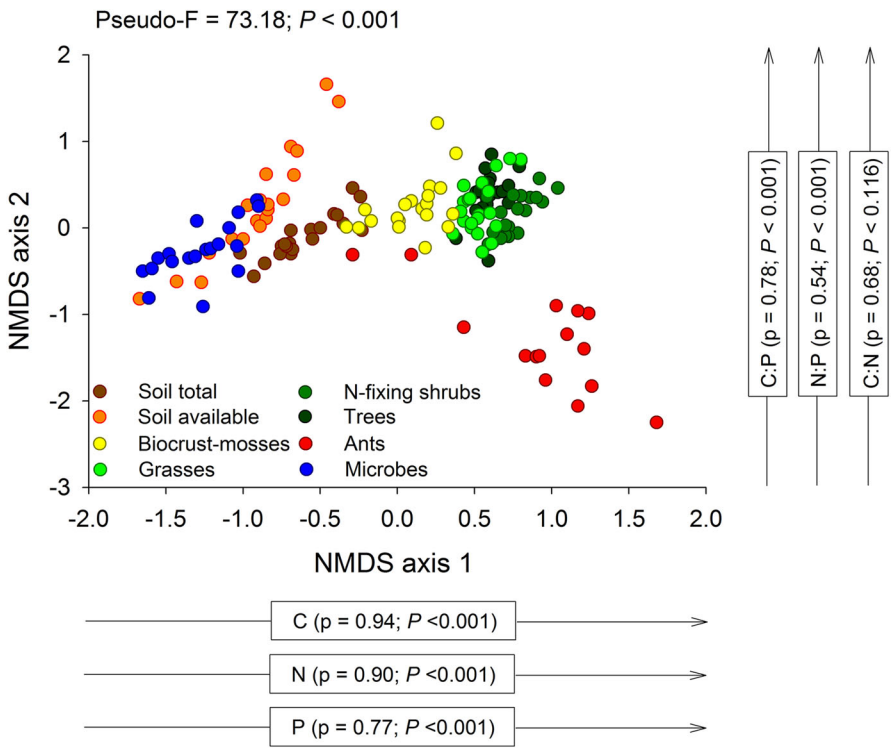

Figure 2. Non-metric multidimensional scaling (NMDS) (stress = 0.08) plots showing the relative differences in C:N:P chemistry and stoichiometry for soil, autotrophic and heterotrophic organisms. Data are mean values ± SE for 22 plots. *Boxes* to the *right* and *below the figure* include significant correlations (Spearman's ρ) between C:N:P concentration and ratios with the NMDS axes.

correlated with the total soil C:P and N:P ratios and positively correlated with those of ants and microbes (Figs. 3 and S2), but was not correlated with those of grasses, N-fixing shrubs and trees. C:P and C:N ratios of mosses were negatively correlated with increasing aridity (Figs. 3 and S2).

At this point, we would like to clarify that, in the case of soil samples we focused on bare ground areas to avoid any confounding effects from plant litter on soil stoichiometry; however, soil chemistry is expected to be highly correlated in the selected microsites across our aridity gradient. For example, preliminary analyses provided evidence that total soil C:N:P concentrations and ratios were highly correlated across microsites (Table S3). Most importantly, the correlations between aridity with total C:N:P concentrations and ratios are similar across different microsites (Table S4). These analyses provide evidence that, in general, our results are not bias by the choice of microsite.

Discussion

Our study provides evidence that increases in aridity differentially decouple C:N:P concentration and stoichiometry in soil microbes, insects, grasses and mosses. In particular, our study suggests a change in the life strategy of heterotrophs from one based on high growth and energy investment (low C:P and N:P ratios) to one based on high structural investment (high C:P and N:P ratios) along the aridity gradient studied. Moreover, we found reductions in leaf C (mosses and grasses) and C:N and C:P ratios (grasses) for non-woody plants along this gradient, which are consistent with previous results from a soil survey conducted in global drylands (Delgado-Baquerizo and others 2013). Only woody plants (trees and shrubs) showed a high homeostasis to aridity, as their C:N:P ratios and concentrations did not change along the aridity gradient studied.

As predicted (Fig. 1), microbial and ant C:P and N:P ratios increased along the aridity gradient studied. In humid environments, maintaining a high microbial and ant activity will require high levels of N and P to continue the production of P- and N-rich organelles and molecules such as ribosomes, ATP, DNA and RNA (that is, high-energy strategy; Elser and others 2000; Sardans and others 2012; Zechmeister-Boltenstern and others 2015). In more arid environments, however, strategies will depend on the ability to resist desiccation for extended periods. Biological activity is known to be reduced with increasing aridity due to water stress in drylands (Whitford 1978; Frenette-Dussault and others 2013; Delgado-Baquerizo and others 2013; Maestre and others 2015). To resist desiccation, it is known that insects can alter their structure by reducing the permeability of the cuticle altering its lipid compo-

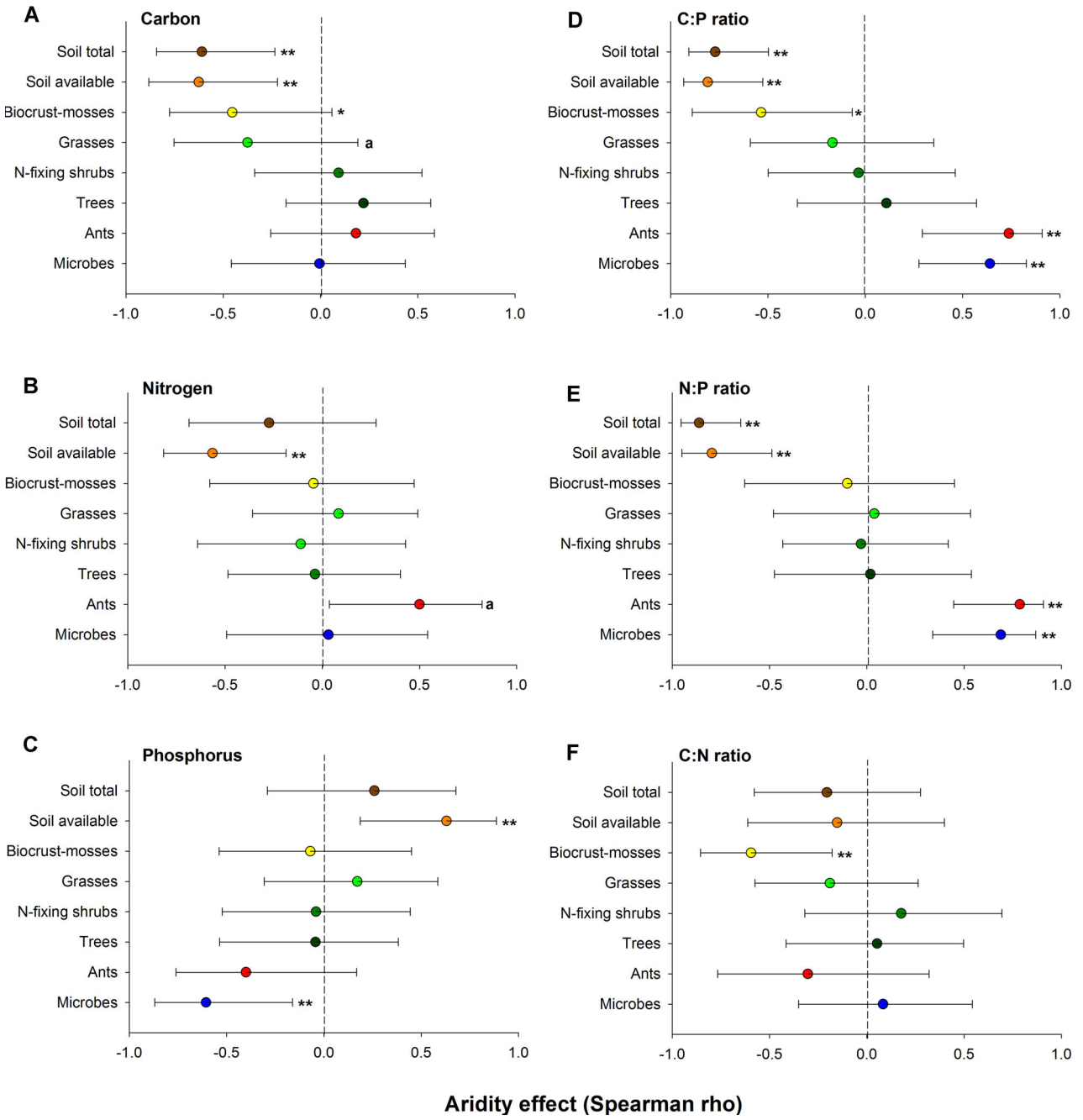

Figure 3. Aridity effects (Spearman's ρ) on C:N:P chemistry and ratios of soil, autotrophic and heterotrophic organisms. The bars around the means are bias-corrected 95% bootstrap confidence intervals. Negative/positive mean Spearman's ρ indicate negative/positive impacts of aridity on a particular C:N:P element and ratio. Significance levels are as follows: $^{a}P < 0.10$; $^{*}P < 0.05$; $^{**}P < 0.01$.

sition and/or enhancing their tolerance to water loss by increasing hemolymph osmolality (Gibbs and others 1997; Weldon and others 2016). Similarly, soil microbes can survive desiccation as dormant inocula by accumulating C- and N-demanding solutes in their cells to reduce water potential and to maintain hydration (Csonka 1989; Schimel and others 2007). Other structures used by soil microbes and insects to resist desiccation include cell walls, structural proteins, fatty acids and waxy molecules, all of them requiring high amounts of C (Gibbs and others 1997; Weldon and others 2016).

Several mechanisms might help to explain the differential responses of C:N:P concentration and stoichiometry of non-woody (grasses and mosses) versus woody (trees and shrubs) plants. In particular, we predicted that larger vascular plants such as trees and N-fixing shrubs are more independent of topsoil water than shorter vascular and non-vascular plants because their well-developed root systems allow them to access moisture stored at deeper layers in the soil (Walter 1939; Ward and others 2013) (Appendix S1). Conversely, shorter vascular and non-vascular plants have smaller (or rudimentary) root systems, which make them more vulnerable to increases in aridity. Dryland mosses, however, lack of a complex root system and are not reliant on soil moisture for hydration, as they have mechanisms to trap water from atmospheric sources (for example, dew and fog; Pan and others 2016). The two-layer hypothesis of Walters (1939) predicts a strong vertical niche partitioning of water, with grasses accessing surface horizons (generally <50 cm deep) while woody plants have a greater access to deeper, subsoil moisture. A recent meta-analysis demonstrated strong support for this phenomenon in environments ranging from deserts to mesic savannas (Ward and others 2013). Thus, woody plants (trees and shrubs) have a greater capacity to obtain water than non-woody plants (mosses and grasses), but also a higher transpiration rate and ability to regulate water loss (Mazzacavallo and Kulmatiski 2015). This greater capacity may help woody plants to maintain photosynthetic rates and hence C fixation. In contrast, shorter vascular and non-vascular plants such as short grasses and mosses will be active for a shorter period in response to low water availability, fixing less atmospheric C (Walters 1939; Ward and others 2013). This would explain the lower C (mosses and grasses) and C:P and C:N ratios (mosses) observed with increasing aridity. These results are consistent with those from a previous study showing a positive correlation between total annual rainfall and the leaf C:N and C:P ratios in a grass species from Chinese arid regions (He and others 2015). We would like to highlight that the relatively lower leaf C concentration in grasses compared to trees and shrubs might be a consequence of the high silicon content often found in grass foliage and which provides some of the structure that dicotyledons obtain from C-rich compounds (Shewmaker and others 1989). This should not bias, however, the conclusions from our study as, if this occurred, this artifact should not alter the C:N:P ratios in grass leaves.

Our results have implications for predicting the potential consequences of increasing aridity on ecosystem functions and services (for example, carbon storage and nutrient cycling) and on long-term life evolution in drylands. For example, our study provides evidence that C (grasses and mosses) and C:N and C:P ratios (mosses) in non-woody plants will decline with increasing aridity (that is, without accounting for dispersal limitations). Some of these changes in C, C:N and C:P stoichiometry in mosses and grasses may be indirectly driven by changes in species composition from mesic to more arid ecosystems (Table S1). Moreover, the cover of grasses (but not mosses; Delgado-Baquerizo and others 2016a) declines with increasing aridity ($\rho_{grasses} = -0.41$, $P = 0.064$) along the same gradient (Delgado-Baquerizo and others 2016a). A lower C fixation by grasses and mosses, with an averaged total ground cover in the studied sites of 25 and 10%, respectively (Delgado-Baquerizo and others 2016a), will likely reduce the capacity of drylands to fix atmospheric C. Although the effect of aridity on small autotrophs is obvious from our data, it is important to highlight the fact that elevated [CO_2] may enhance water use efficiency (WUE) in C3 plants and therefore C fixation in drylands (Evans and others 2014), which may potentially mitigate some of the reported negative effects of aridity on leaf C and C:N and C:P ratios. Whether an increase in WUE due to rising CO_2 can compensate for the negative effects of increased aridity on water availability and C fixation is largely unknown. However, it has been recently observed that increased [CO_2] cannot fully compensate for the negative impacts of aridity on plant growth (Brookshire and Weaver 2016).

Additionally, shifts in tissue stoichiometry of soil microbes and mosses in response to increasing aridity will likely influence the rates at which essential processes such as soil organic matter decomposition and mineralization occur in drylands, which are largely controlled by litter quality and microbial stoichiometry. For example, a reduction in leaf tissue C:N ratio with increasing aridity may promote higher mineralization rates beneath mosses, leading to nutrient losses to the subsoil and atmosphere (Dijkstra and others 2012). More than impacting ecosystem functioning in the medium term (years to centuries), increases in aridity could promote evolutionary long-term changes in the stoichiometry of soil microbes, insects and short plants. A recent study highlighted the importance of human legacies for plant stoichiometry during domestication and their implications for ecosystem functioning (that is, nutrient

cycling; Delgado-Baquerizo and others 2016b). Similarly, changes in life stoichiometry with increasing aridity may condition long-term evolutionary trends in drylands by selecting plants, microbes and insects with different levels of C, N and P in their structures, potentially altering ecosystem structure and functioning (Peñuelas and others 2012).

Conclusions

To our knowledge, our results provide, for the first time, an assessment of the effects of aridity on the stoichiometry of multiple aboveground (ants, woody and non-woody plants) and belowground (soil microbes) communities. Our results suggest that increases in aridity by the end of this century will likely alter the C:N:P stoichiometry of heterotrophs (ants and microbes), non-woody plants and in soil, but will not affect that one from woody plants. In particular, our results indicate that increases in aridity will likely increase the C:P and N:P ratios of microbes and ants and will decrease the concentration of C and the C:N and C:P ratios in mosses and/or short grasses. Our findings strongly suggest that the response of C:N:P stoichiometry of multiple trophic levels needs to be considered simultaneously if we want to properly assess ecological responses to a more arid world.

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Data Accessibility

Data associated with this paper have been deposited in figshare: https://figshare.com/s/d736cb67a3397d3c7f1c (10.6084/m9.figshare.5056486).

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