Global Ecology and Biogeography A Journal of Macroecology
Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2016) **25**, 36–45

RESEARCH PAPER

Human impacts and aridity differentially alter soil N availability in drylands worldwide

Manuel Delgado-Baquerizo[1,2]*, Fernando T. Maestre[1], Antonio Gallardo[3], David J. Eldridge[4], Santiago Soliveres[1,5], Matthew A. Bowker[6], Ana Prado-Comesaña[3], Juan Gaitán[7], José L. Quero[8], Victoria Ochoa[1], Beatriz Gozalo[1], Miguel García-Gómez[1], Pablo García-Palacios[1,9], Miguel Berdugo[1], Enrique Valencia[1], Cristina Escolar[1], Tulio Arredondo[10], Claudia Barraza-Zepeda[11], Bertrand R. Boeken[12], Donaldo Bran[7], Omar Cabrera[13], José A. Carreira[14], Mohamed Chaieb[15], Abel A. Conceição[16], Mchich Derak[17], Ricardo Ernst[18], Carlos I. Espinosa[13], Adriana Florentino[19], Gabriel Gatica[20], Wahida Ghiloufi[15], Susana Gómez-González[21], Julio R. Gutiérrez[11,22,23], Rosa M. Hernández[24], Elisabeth Huber-Sannwald[10], Mohammad Jankju[25], Rebecca L. Mau[26], Maria Miriti[27], Jorge Monerris[28], Ernesto Morici[18], Muchai Muchane[29], Kamal Naseri[25], Eduardo Pucheta[20], Elizabeth Ramírez[24], David A. Ramírez-Collantes[30], Roberto L. Romão[16], Matthew Tighe[31], Duilio Torres[32], Cristian Torres-Díaz[21], James Val[33], José P. Veiga[34], Deli Wang[35], Xia Yuan[35] and Eli Zaady[36]

[1]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Calle Tulipán Sin Número, Móstoles 28933, Spain, [2]Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, NSW 2751, Australia, [3]Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Carretera de Utrera, Km 1, Sevilla 41013, Spain, [4]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia, [5]Institute of Plant Sciences, University of Bern, Alterbengrain 21, Bern 3013, Switzerland, [6]School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA, [7]Instituto Nacional de Tecnología Agropecuaria, Estación Experimental San Carlos de Bariloche, Casilla de Correo 277 (8400), Bariloche, Río Negro, Argentina, [8]Departamento de Ingeniería Forestal, Campus de Rabanales Universidad de Córdoba, Carretera Nacional, Km 396, Córdoba 14071, Spain, [9]Centre d'Ecologie Fonctionnelle et Evolutive, CEFE-CNRS, 1919 Route de Mende, Montpellier 34293, France, [10]División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica, Código Postal 78210, San Luis Potosí, San Luis Potosí, Mexico, [11]Departamento de Biología, Universidad de La Serena, Casilla 599, La Serena, Chile, [12]Wyler Department of Dryland Agriculture, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84990, Israel, [13]Departamento de Ciencias Naturales, Universidad Técnica Particular de Loja, San Cayetano Alto, Marcelino Champagnat, Loja, Ecuador, [14]Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaen, Jaen 23071, Spain, [15]Faculty of sciences, UR Vegetal Diversity and Arid Land Ecosystems, University of Sfax, Route de Sokra, Km 3.5, Boîte Postale 802, Sfax 3018, Tunisia, [16]Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia 44036-900, Brazil, [17]Direction Régionale des Eaux et Forêts et de la Lutte Contre la Désertification du Rif, Avenue Mohamed 5, Boîte Postale 722, Tétouan 93000, Morocco, [18]Facultad de Agronomía, Universidad Nacional de La Pampa, Casilla de Correo 300, Santa Rosa, La Pampa 6300, Argentina, [19]Instituto de Edafología, Facultad de Agronomía, Universidad Central de Venezuela, Ciudad Universitaria, Caracas, Venezuela, [20]Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Rivadavia, San Juan J5402DCS, Argentina, [21]Laboratorio de Genómica y Biodiversidad, Departamento de Ciencias Básicas, Universidad del Bío-Bío, Casilla 447, Chillán, Chile, [22]Instituto de Ecologia y Biodiversida, Casilla 653, Santiago, Chile, [23]Centro de Estudios Avanzados en Zonas Aridas, La Serena, Chile, [24]Laboratorio de Biogeoquímica, Centro de Agroecología Tropical, Universidad Experimental Simón Rodríguez, Apdo 47925, Caracas, Venezuela, [25]Department of Range and Watershed Management, Faculty of Natural Resources and Environment, Ferdowsi University of Mashhad, Azadi Square, Mashhad 91775-1363, Iran, [26]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA, [27]Department of Evolution, Ecology and Organismal Biology, Ohio State University, 318 West 12th Avenue, Columbus, OH 43210, USA, [28]Pavillon des Sciences Biologiques, Département des Sciences Biologiques, Université du Québec à Montréal, 141 Président-Kennedy, Montréal, QC H2X 3Y5, Canada, [29]Zoology Department, National Museums of Kenya, 78420-00500 Ngara Road, Nairobi, Kenya, [30]Production Systems and the Environment Sub-Program, International Potato Center, Apartado 1558, Lima 12, Peru, [31]Department of Agronomy and Soil Science, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia,

ABSTRACT

Aims Climate and human impacts are changing the nitrogen (N) inputs and losses in terrestrial ecosystems. However, it is largely unknown how these two major drivers of global change will simultaneously influence the N cycle in drylands, the largest terrestrial biome on the planet. We conducted a global observational study to evaluate how aridity and human impacts, together with biotic and abiotic factors, affect key soil variables of the N cycle.

Location Two hundred and twenty-four dryland sites from all continents except Antarctica widely differing in their environmental conditions and human influence.

Methods Using a standardized field survey, we measured aridity, human impacts (i.e. proxies of land uses and air pollution), key biophysical variables (i.e. soil pH and texture and total plant cover) and six important variables related to N cycling in soils: total N, organic N, ammonium, nitrate, dissolved organic:inorganic N and N mineralization rates. We used structural equation modelling to assess the direct and indirect effects of aridity, human impacts and key biophysical variables on the N cycle.

Results Human impacts increased the concentration of total N, while aridity reduced it. The effects of aridity and human impacts on the N cycle were spatially disconnected, which may favour scarcity of N in the most arid areas and promote its accumulation in the least arid areas.

Main conclusions We found that increasing aridity and anthropogenic pressure are spatially disconnected in drylands. This implies that while places with low aridity and high human impact accumulate N, most arid sites with the lowest human impacts lose N. Our analyses also provide evidence that both increasing aridity and human impacts may enhance the relative dominance of inorganic N in dryland soils, having a negative impact on key functions and services provided by these ecosystems.

DOI: 10.1111/geb.12382
 http://wileyonlinelibrary.com/journal/geb

[32]Departamento de Química y Suelos, Decanato de Agronomía, Universidad Centroccidental 'Lisandro Alvarado', Barquisimeto 3001, Venezuela, [33]Office of Environment and Heritage, Post Office Box 363, Buronga, NSW 2739, Australia, [34]Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2, Madrid 28006, Spain, [35]Institute of Grassland Science, Northeast Normal University, Key Laboratory of Vegetation Ecology, Ministry of Education, Changchun, Jilin 130024, China, [36]Department of Natural Resources, Agriculture Research Organization, Gilat Research Center, Ministry of Agriculture, Mobile Post, Negev 85280, Israel

*Correspondence: Manuel Delgado-Baquerizo, Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, NSW 2751, Australia.
E-mail: m.delgadobaquerizo@uws.edu.au

Keywords
Aridity, depolymerization, global change, human impacts, mineralization, N cycle.

INTRODUCTION

Human activities such as grazing, fertilization, intensive agriculture and the combustion of fossil fuels are changing the inputs to, and losses from, the nitrogen (N) cycle in terrestrial ecosystems globally (Vitousek *et al.*, 1997; Cui *et al.*, 2013). Anthropogenic inputs of N have already doubled the total amount of N fixed naturally by terrestrial and aquatic ecosystems, with current annual rates of both organic and inorganic N deposition of about 124 Tg N year^{-1} (Gruber & Galloway, 2008; Schlesinger, 2009; Cornell, 2011). Human pressure on the N cycle is expected to rise during this century because of the predicted increase in global population by 36% over the next 40 years (Godfray *et al.*, 2010) and the intensification of land use required to support the subsequent demand for food (OECD-FAO, 2011), which is estimated to increase by 70–100% by 2050 (World Bank, 2008). In parallel to the increase in N inputs derived from human activities, ongoing climate change will increase the degree of aridity experienced by drylands (arid, semi-arid and dry-subhumid ecosystems) world-wide, which is predicted to increase their total global extent by 10% by the end of this century (Feng & Fu, 2013). Increasing aridity has been shown to reduce the availability of soil N in drylands globally, and to reduce the pools of organic N in these ecosystems (Schlesinger *et al.*, 1990; Delgado-Baquerizo *et al.*, 2013a). These changes can further exacerbate the negative effects of land degradation and desertification in drylands, which are estimated to currently affect more than 250 million people, mostly in developing countries (Reynolds *et al.*, 2007).

Human activities (i.e. air pollution and changes in land use) and climate change are key drivers of ongoing global environmental change (Gruber & Galloway, 2008; Schlesinger, 2009; Canfield *et al.*, 2010; Liu *et al.*, 2010; Bai *et al.*, 2013) and are interrelated in complex ways. These drivers of global change may act in opposition or interact to accelerate their effects on natural communities. The combined impacts derived from human activities and climate change may create a more arid environment that is also characterized by reduced biological control of the N cycle (Schlesinger *et al.*, 1990). For instance, direct anthropogenically driven disturbances (e.g. overgrazing) and increases in aridity may have a negative impact on plant growth in drylands (Gruber & Galloway, 2008; Delgado-Baquerizo *et al.*, 2013a), thereby reducing inputs of organic N in these ecosystems. The impacts of human activities on the N cycle in drylands have been largely studied at local scales. For example, Baker *et al.* (2001) concluded that the urban and agricultural components of the ecosystem were an order of magnitude higher than natural inputs in Phoenix, AZ, increasing the amount of N in soil and groundwater pools and promoting losses of N to rivers. Similarly, nutrient enrichment derived from human activities has also been observed to locally enhance N mineralization in the Sonoran Desert (Hall *et al.*, 2011). Nevertheless, little is known about how the interaction between increasing aridity and human impacts will affect the concentration of available N for plants and microorganisms, as well as the dominance of different forms of N in global drylands.

Nitrogen is, after water, the most important factor limiting net primary production and decomposition of organic matter in drylands (Robertson & Groffman, 2007; Schlesinger & Bernhardt, 2013). The N cycle is therefore crucial for ecosystem functioning and the provision of ecosystem services in these areas (Robertson & Groffman, 2007; Compton *et al.*, 2011; Schlesinger & Bernhardt, 2013). As drylands occupy over 40% of earth's land surface (MEA, 2005), understanding how direct and indirect effects from climatic (i.e. aridity), biophysical (i.e. soil texture, pH and plant cover) and anthropogenic (i.e. human-induced climate change, air pollution and land use changes) drivers jointly affect the N cycle is crucial for improving our ability to predict the ecological consequences of ongoing global change for terrestrial ecosystems (Schlesinger *et al.*, 1990; Gruber & Galloway, 2008; Chen *et al.*, 2013).

We conducted a global observational study of 224 dryland ecosystems from all continents except Antarctica to evaluate how aridity and human impacts, together with biotic (plant cover) and abiotic (soil texture and pH) factors, will affect total N, dissolved organic N, ammonium and nitrate concentrations, the dissolved organic N to dissolved inorganic N (DON:DIN) ratio and the potential net mineralization rate of dryland soils. These variables were selected because they are good proxies for N availability and dominance of N forms within soils (Schimel & Bennett, 2004; Delgado-Baquerizo & Gallardo, 2011). We hypothesized that: (1) total N concentration in soils would be enhanced by human impacts (estimated indirectly using proxies) but would decline with aridity (Delgado-Baquerizo *et al.*, 2013a) and (2) aridity and human impacts will negatively affect the biological control of the N cycle (via mechanisms such as the reduction in total plant cover), resulting in an increasing dominance of inorganic forms of N and processes (i.e. mineralization) in dryland soils (Schlesinger *et al.*, 1990).

MATERIALS AND METHODS

Study area

This study was restricted to dryland ecosystems, defined as regions with an aridity index (AI; equal to precipitation/ potential evapotranspiration) between 0.05 and 0.65 (UNEP, 1992). Original field data were collected at 224 sites located in 16 countries from all continents except Antarctica (Maestre *et al.*, 2012). The sites surveyed encompass a wide variety of vegetation types typically found in drylands, including grasslands, shrublands, savannas, dry seasonal forests and open woodlands dominated by trees. Mean annual precipitation and temperature of the study sites ranged from 66 to 1219 mm and from −1.8 to 27.8°C, respectively. Maestre *et al.* (2012) give an interactive map with a general description of the study sites.

Climatic, abiotic, plant and nitrogen variables measured

Data collection was carried out between February 2006 and December 2010 according to a standardized sampling protocol. The cover of vascular plants at each site was measured using four 30-m transects and the line-intercept method, as described in Maestre *et al.* (2012). The coordinates of each plot were recorded *in situ* with a portable global positioning system, and were standardized to the WGS84 ellipsoid for visualization and analyses. Aridity (1 – Aridity index) was estimated using the Global Aridity Index (Global-Aridity) dataset (http://www.cgiar-csi.org/data/global-aridity-and-pet-database; Zomer *et al.*, 2008), which is based on the interpolations provided by the WorldClim climatic database (Hijmans *et al.*, 2005). Soils (0–7.5 cm depth) were sampled during the dry season under two different microsites: the canopy of the dominant perennial plants and in open areas devoid of vascular vegetation (10–15 samples were sampled per site, over 2600 samples in total). Soil samples in plant microsites were always collected under the canopy and close to the centre of the plant to avoid spatial patterns in N availability from the bole to the canopy edge. After field collection, the soil samples were taken to the laboratory, where they were sieved (2-mm mesh), air-dried for 1 month and stored in this condition until laboratory analyses. For logistical reasons all the soil analyses in this study were carried out with air-dry samples. Previous works have shown that in drylands such as those we studied, air drying and further storage of soils does not appreciably alter the functions of interest in this study (Zornoza *et al.*, 2006, 2009). It is also important to note that our sampled soils were collected when the soil was in this dry state, and that low moisture values are found in dryland soils during most of the year (e.g. Maestre *et al.*, 2013). Thus, the potential bias induced by our drying treatment is expected to be minimal.

To avoid problems associated with the use of multiple laboratories when analysing the soils from different sites, and to facilitate the comparison of results between them, dried soil samples from all the countries were shipped to Spain for analysis. A composite sample per microsite (open areas or soil under the canopy of the dominant perennial plants) and site was analysed for sand, clay and silt content according to Kettler *et al.* (2001). Soil pH was measured in all the soil samples with a pH meter, in a 1:2.5 mass:volume soil and water suspension. We also measured multiple variables from the N cycle [total N, mineralization rate, DIN (the sum of NH_4^+ and NO_3^-) and DON]. These variables were selected because they are good proxies of N availability and the dominance of different forms of N within soils (Schimel & Bennett, 2004; Delgado-Baquerizo & Gallardo, 2011). Soil samples (2.5 g of soil) were extracted with 0.5 M K_2SO_4 in a ratio 1:5. Soil extracts were shaken in an orbital shaker at 200 r.p.m. for 1 h at 20 °C and filtered to pass a 0.45-μm Millipore filter (Jones & Willett, 2006). The filtered extract was kept at 4 °C until colorimetric analyses. Using the indophenol blue method (Sims *et al.*, 1995), we estimated concentrations of ammonium and nitrate (colorimetrically) and available N (after potassium persulphate digestion in an autoclave at 121 °C over 55 min; Sollins *et al.*, 1999). DON was determined as the difference between available N and inorganic N (the sum of ammonium and nitrate). The ratio DON:DIN was determined from these data. To estimate potential mineralization rate, air-dried soil samples were re-wetted to reach 80% of their water-holding capacity and incubated in the laboratory for 14 days at 30 °C (Allen *et al.*, 1986). The potential net N mineralization rate was estimated as the difference between initial and final inorganic N (Delgado-Baquerizo & Gallardo, 2011). We acknowledge that 80% water holding capacity and 30 °C may not meet the optimum conditions for all the different groups of microorganisms conducting mineralization in the different soil samples. Despite this fact, using these conditions has many advantages. For example, potential net mineralization (as in Allen *et al.*, 1986) has largely been used over the last few decades, and allows us to compare our data with those from other studies. In addition, even when these potential conditions may not be optimal for different groups of microorganisms they have been largely considered as the potential conditions for mineralization in soil (Allen *et al.*, 1986). In addition, operating under these conditions gives us extremely reliable information on the availability of inorganic N in soil (Durán *et al.*, 2012). Finally, total N was obtained using a CN analyser (LECO CHN628 Series, LECO Corporation, St Joseph, MI, USA). All the soil variables used were averaged to obtain site-level estimates by using the mean values observed in bare ground and vegetated areas weighted by their respective cover at each site (Maestre *et al.*, 2012). All the analyses for total N were carried out at the University of Jaén (Jaén, Spain), soil texture and pH were analysed at Rey Juan Carlos University (Móstoles, Spain) and the remaining N variables were analysed at Pablo de Olavide University (Seville, Spain).

Assessing human impacts

Quantitative estimates of the magnitude of human impacts in natural ecosystems at global scales are difficult to obtain due to the lack of available data and the wide range of processes affected by human activities, their different spatial scales and the interactions among them (Beelen *et al.*, 2013). We used two complementary approaches to estimate the impacts of human activities on the N cycle. First, we estimated such impacts indirectly by measuring four variables at each surveyed plot: (1) average proximity (in km) to the nearest northern, southern, eastern and western paved roads, (2) average proximity (in km) to the four nearest towns/cities, (3) average population of these towns/cities in the last available census (number of people), and (4) population density (number of people·per km^2) of the province or region of each plot in the most recent available census. Due to the large distances between some of our study sites and the nearest towns/cities we considered the four closest cities to our plots, as an average value of the local human impact. Distances to nearest roads and cities/towns are classic proxies of human impacts on ecosystem structure and functioning (Schlesinger & Harley, 1992; Gill *et al.*, 1996; Drechsel *et al.*, 2001; Liu *et al.*, 2010; Beelen *et al.*, 2013). Similarly, soil N depletion derived from land-use changes have been observed to be linked to increasing size of the local human population (Drechsel *et al.*, 2001; Canfield *et al.*, 2010). Thus, we assumed that the magnitude of human impacts on the N cycle, such as N deposition and/or soil erosion, would be positively related to the proximity of each site to the nearest city/town and paved road, and directly related to the number of people in this city/town and the population density (Drechsel *et al.*, 2001; Gilbert *et al.*, 2007; Gadsdon & Power, 2009; Liu *et al.*, 2010; Beelen *et al.*, 2013).

The four surrogates of human impacts considered were highly correlated. Thus, we conducted a principal components analysis (PCA) to reduce them to independent components. Before conducting the PCA, all the proxies for human impact were log-transformed to normalize them. We retained the first two components from the PCA for further analyses; these had an eigenvalue greater than 1 and together explained 80.5% of the variance in the PCA. The first component of the PCA (HC1) was highly related to the average distance to the four nearest towns/cities from each plot (Pearson's $r = 0.96$), the average distance to the nearest northern, southern, eastern and western paved roads from each plot (Pearson's $r = 0.76$) and the population density of the province of each plot in the most recent available census (Pearson's $r = 0.71$). The second component of the PCA (HC2) was highly related to the average population size of the four nearest towns/cities during the most recent census (Pearson's $r = 0.90$). Both HC1 and HC2 are positively related to other indices of human impact from the literature, such as the human influence index (Spearman $\rho = 0.70$, $P < 0.001$ and $\rho = 0.14$, $P = 0.044$, respectively) and the human footprint index (Spearman $\rho = 0.69$, $P < 0.001$ and $\rho = 0.13$ $P = 0.051$, respectively), available from the Last of the Wild Data, Version 2 (Last of the Wild Data, 2005). Geographical distances were obtained with Google Earth® (www.google.com/earth/index.html), while population data were gathered from the official statistics for each country (see Table S1).

Secondly, we estimated inorganic N deposition, fertilizer application and the amount of N produced in livestock manure in each of our plots. Information on inorganic N deposition, N in fertilization and N in manure was collected at a global scale using the available maps from Dentener *et al.* (2006) and Potter *et al.* (2011). Information on each of these indices was collected for each site location using ESRI ArcMap 10 (Redlands, CA, USA). Information on the relationships between the different human impact variables evaluated is given in Table S2.

Statistical analyses

We used structural equation modelling (SEM) to determine the relative importance of human impacts (a total of five human impact indices: HC1, HC2, N in fertilization and manure and inorganic N in deposition), aridity, pH, sand content, plant cover and the spatial influence (distance from the equator and longitude) on the different N variables evaluated. We first established an a priori model (Fig. S1) based on the known effects and relationships among the drivers of the N cycle (Methods S1). Total N, concentrations of ammonium, nitrate and DON, the DON:DIN ratio and pH were log-transformed to improve linearity in the relationships between the variables in our SEM models. Similarly, plant total cover and sand content were square-root transformed. We found that all N metrics, sand content, N in fertilization and HC1 displayed unimodal relationships with aridity. To introduce these second-order polynomial relationships into our SEM model, we calculated the square of aridity and introduced it into our model using a composite variable (Fig. S1). Similarly, the human impact and spatial influence metrics were also included as composite variables. The use of composite variables does not alter the underlying SEM model but collapses the effects of multiple conceptually related variables into a single composite effect, aiding interpretation of model results (Grace, 2006). We also examined the distributions of all of our endogenous variables (those with arrows pointing to them within the a priori model structure, Fig. S1) and tested their normality. Because some of the variables introduced were not normally distributed, the probability that a path coefficient differs from zero was tested using bootstrap tests (Schermelleh-Engel *et al.*, 2003). Our a priori model structure gave a satisfactory fit to our data, as suggested by non-significant χ^2 values ($\chi^2 = 2.97$, $P = 0.56$; four degrees of freedom in all cases), nonparametric bootstrap $P = 0.59$ and by values of the root mean square error of approximation equal to 0.00 with $P = 0.77$.

We also calculated the standardized total effects (direct plus indirect effects from the structural equation model) of human

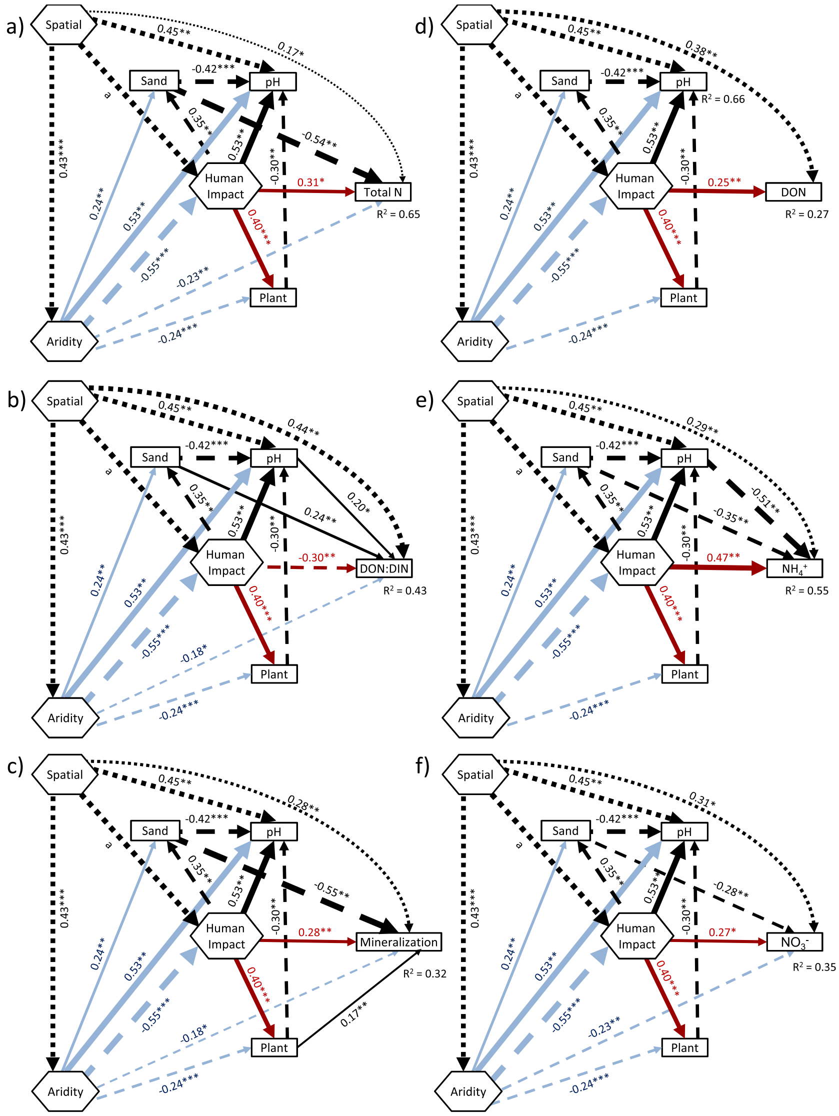

Figure 1 Effects of aridity (blue/light grey arrows), human impacts (red/dark grey arrows), pH, sand content, plant cover and spatial influence (black arrows) on: total N (a), DON:DIN ratio (b), mineralization rate (c), DON (d), NH_4^+ (e) and NO_3^- (f). Numbers adjacent to the arrows indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. R^2 denotes the proportion of variance explained. For graphical simplicity, factors influencing human impacts (a) are: Spatial → HC1 = 0.23**; Spatial → HC2 = –0.45***; Spatial → N deposition = 0.40***; Spatial → N in fertilization = 0.49***; Spatial → N in manure = –0.14*. Significance levels are as follows: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

impacts (HC1, HC2, N in fertilization and manure and inorganic N in deposition), aridity, pH, sand content, plant cover and spatial influence (longitude and distance from the equator) on the selected N metrics (Grace, 2006). All the SEM analyses were conducted using the software AMOS 20 (IBM SPSS Inc, Chicago, IL, USA). The raw data used in study are available in Appendix S1.

RESULTS

Sand content, pH and total plant cover in our study sites ranged from 5.36 to 97.94%, 4.13 to 9.21 and 2.83 to 82.88% respectively. Similarly, for the studied N variables, total N ranged from 0.01 to 0.45%, ammonium from 0.82 to 55.86 mg N kg^{-1} soil, nitrate from 0 to 92.07 mg N kg^{-1} soil, DON from 1.24 to 43.31 mg N kg^{-1} soil and potential mineralization rate from –2.13 to 5.01 mg N kg^{-1} soil day^{-1}.

Aridity was directly and negatively related to soil total N, whereas our surrogates of human impacts were positively related to total N (Fig. 1a). Interestingly, HC1, inorganic N deposition and N in fertilization and manure were negatively related to aridity (Table 1), but aridity and HC2 were unrelated (Table 1). Aridity and human impacts, together with sand content, were the most important factors controlling soil total N, as indicated by the size of their total effects (Fig. 2a). Moreover, the total (direct plus indirect) effect of distance to towns and roads (HC1) and of N in fertilization and deposition on soil total N was opposite to that of N in manure and HC2 (Fig. 2a). In absolute terms, however, the impacts of HC1 and N in fertilization and deposition were higher than that of N in manure and HC2, resulting in a net total positive effect of human impacts on this variable (Fig. 2a).

Increases in both aridity and human impacts were associated with reductions in the DON:DIN ratio (Figs 1b & 2b). In addition, increases in human impacts were related to increases in potential net mineralization rates (Figs 1c & 2c). Our different surrogates of human impacts (HC1, HC2, inorganic N deposition, N in fertilization and manure) produced different and

Table 1 Correlation coefficients (Spearman ρ, P-value in brackets) between aridity, the nitrogen (N) variables evaluated and the surrogates of human impacts used in this study. HC1 and HC2 are the first and second components of a principal component analysis from four proxies of human impacts (proximity to urban areas, paved roads, population density and population size). Inorganic N deposition (ND), fertilizer application (NF) and the amount of N in livestock manure production (NM) were collected from Dentener *et al.* (2006) and Potter *et al.* (2011). $n = 224$.

	Aridity	HC1	HC2	NF	NM	ND
Aridity		−0.245 (<0.001)	−0.008 (0.900)	−0.247 (<0.001)	−0.234 (<0.001)	−0.432 (<0.001)
Total N	−0.529 (<0.001)	0.425 (<0.001)	−0.075 (0.263)	0.508 (<0.001)	0.307 (<0.001)	0.556 (<0.001)
DON:DIN	0.068 (0.314)	−0.197 (0.003)	0.000 (0.997)	−0.224 (0.001)	−0.035 (0.601)	−0.190 (0.004)
Mineralization	−0.193 (0.004)	0.239 (<0.001)	0.082 (0.221)	0.376 (<0.001)	0.200 (0.003)	0.198 (0.003)
DON	−0.067 (0.318)	0.052 (0.441)	−0.079 (0.237)	0.127 (0.057)	0.149 (0.025)	−0.002 (0.974)
NH_4^+	−0.391 (<0.001)	0.476 (<0.001)	0.130 (0.053)	0.576 (<0.001)	0.376 (<0.001)	0.352 (<0.001)
NO_3^-	0.021 (0.758)	0.264 (<0.001)	−0.180 (0.007)	0.321 (<0.001)	0.040 (0.547)	0.161 (0.016)

DON, dissolved organic N; DIN, dissolved inorganic N.

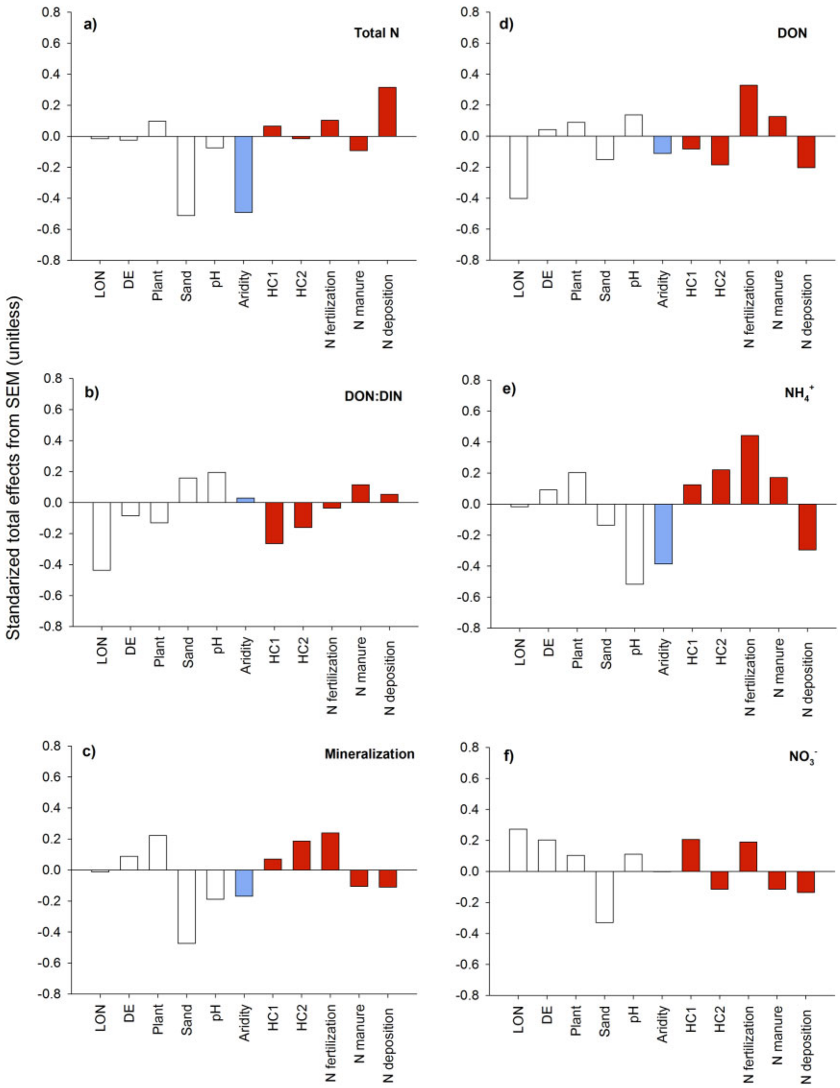

Figure 2 Standardized total effects (direct plus indirect effects) derived from the structural equation modelling, including the effects of aridity (Aridity), percentage of sand (sand), pH, plant cover (Plant), distance from equator (DE) and longitude (LON) and human impacts (HC1, HC2, N in fertilization, N in manure and N deposition; see Materials and Methods for details) on the total N (a), DON:DIN ratio (b), potential mineralization rate (c), DON (d) NH_4^+ (e) and NO_3^- (f).

opposite relationships with DON and soil nitrate, although both were associated with increasing ammonium concentrations (Fig. 2e).

DISCUSSION

Impacts of aridity and human activities on soil total N

Although human activities should increase the N budget world-wide (Galloway *et al.*, 2008), our results suggest that the increases in aridity forecast for large areas of the planet (Feng & Fu, 2013) will counteract such N increments in dryland soils. Of particular interest was the observed negative relationship found between aridity and our surrogates of human impacts (Table 1). This is probably derived from the constraints that aridity, and hence reduction in water availability, generally impose on human activities and urban development (Whitford, 2002; Schwinning & Sala, 2004). The high negative relationship between aridity and our human impact surrogates suggests that there is a current spatial disconnection between the impacts of aridity, which may favour N losses, and those of human activities, which may favour N accumulation, in different dryland regions (Liu *et al.*, 2010). Thus, at the global scale, N limitation will tend to increase in the driest regions, but N enhancement due to human activities in the least arid drylands may counteract any trend towards greater N limitation. It can be argued that demand for N may from plants may decline at greater aridity levels because of declining plant cover; however, it is well known that N can still be an important factor limiting plant growth even in driest lands (Schlesinger *et al.*, 1990; Robertson & Groffman, 2007; Schlesinger & Bernhardt, 2013). Nitrogen is also critically important for other abundant biotic components in drylands, such as biological soil crusts and microbial communities (Schlesinger *et al.*, 1990; Thomas *et al.*, 2011; Delgado-Baquerizo *et al.*, 2013a). In addition, aridity and HC2 were unrelated, suggesting that increasing aridity is related to more to urban sprawl (HC1) but not to population density per se (HC2; Mainguet, 1999). In addition, the negative impacts of N in manure on total N may be related to erosion caused by grazing on our plots (Seagle *et al.*, 1992). We stress that the spatial distribution of our plots did not cover areas where this pattern may not hold, such as large, rapidly growing urban desert areas (e.g. Phoenix or Las Vegas in the USA; Kane *et al.*, 2014) or semi-arid areas with intensive agricultural practices (e.g. Almería in south-east Spain; Aznar-Sánchez & Galdeano-Gómez, 2011). In addition, it may be argued that we are lacking other important human impact surrogates, such as fire, in our study. Unfortunately, appropriate fire indices separating human-derived and natural fires are difficult to find at a global scale. In addition, a recent study suggested that burned areas are negatively related to human population densities and thus may not be a good metric of the human impact on nutrient cycling (Bistinas *et al.*, 2014). We also acknowledge the limitations of the observational approach followed, which does not allow us to demonstrate causal relationships. However, we believe that our study provides a good snapshot of the status of the N cycle at the global scale in drylands as it reveals how the combined effects of aridity and human disturbance can affect N concentrations and the dominance of relative N forms in dryland soils in an integrated way.

Inorganic N accumulation derived from aridity and human impacts

Increasing human impacts resulted in direct and total negative effects on the DON:DIN ratio, and a total positive effect on potential net mineralization rates (i.e. from HC1, HC2 and N in fertilization). Thus, any increase in human impacts is likely to lead to a greater dominance of inorganic forms of N in drylands. This scenario is compatible with both the observed loss of biological control of the N cycle derived from climate change suggested by Schlesinger *et al.* (1990) and Delgado-Baquerizo *et al.* (2013a), and with the trend towards a stage of inorganic N saturation in terrestrial ecosystems as a consequence of anthropogenic N deposition (Gruber & Galloway, 2008; Schlesinger, 2009; Chen *et al.*, 2013). An increase in aridity has been suggested to reduce the net depolymerization rate (DON production) in the most arid areas, probably linked to the low precipitation and plant cover of these environments (Schlesinger *et al.*, 1990), which would increase the dominance of inorganic forms of N. This was supported by the observed direct negative relationship between aridity and DON:DIN. Nevertheless, this direct negative effect was counteracted by the indirect positive effects on the DON:DIN ratio mediated through sand content and pH (Fig. 1b). As a consequence, the total effect of aridity on the dominance of dissolved organic versus inorganic N forms was negligible (Fig. 2b, Table 1). However, our results suggest that rapid changes in aridity, such as those expected for this century, which are not likely to affect pedogenic properties such as soil pH and texture in the short term, may affect the DON:DIN ratio in dryland soils (Schlesinger *et al.*, 1990). Conversely, proximity to human populations (HC1) was the most important factor controlling variations in the DON:DIN ratio (Fig. 2b). This decrease in the DON:DIN ratio with increasing human impacts may be also driven by the increase in inorganic N inputs linked to human activities such as fertilizer production (Fig. 2; Cornell, 2011). An increase in inorganic N in soils may have a negative impact on the functioning and services provided by drylands world-wide. For example, Delgado-Baquerizo *et al.* (2013b) found that inputs of inorganic N were negatively linked to microbial functional diversity and N depolymerization (the production of DON), and thus may also reduce the uptake of organic N by plants and microorganisms in these ecosystems (Warren, 2009).

Shifts in the different forms of N derived from human impacts

Interestingly, while aridity had an overall total negative effect on most of the N variables studied here, different surrogates of human impacts were related to the different forms of N in very different ways. For example, we found a relatively strong total positive relationship between N in fertilization and N in manure and DON concentrations in dryland soils. Organic fertilization and manure application are well known to increase the amount of DON in soils, and may be altering the abundance of this form of N in drylands world-wide. In addition, HC1 and N in fertilization were the only human impacts showing a total positive effect on the concentrations of soil nitrate, suggesting the importance of fertilization with both reduced and oxidized N in global drylands. Because our sites are not located in agricultural areas, the effect of highly populated towns surrounding our plots (HC2) should be related more to the use of these drylands for grazing and wood harvesting than to more intensive human uses. Intensive land management may result in DON and nitrate leaching into streams and groundwater, which may pollute them (Gruber & Galloway, 2008; Schlesinger, 2009; Chen *et al.*, 2013). Interestingly, N deposition was the only human surrogate showing total negative effects on DON, ammonium and nitrate despite having a total positive effect on the total soil N. This striking result suggests that N derived from deposition may be a preferable form of N for plants and microbes in dryland ecosystems, which are very poor in N (Schlesinger *et al.*, 1990). In fact, the positive effect of human impacts on plant cover that we found supports this idea. In this respect, higher N deposition may lead to a higher uptake of N by plants and microbes, promoting the accumulation of total N in the soil in the long term due to increased litter decomposition (Schlesinger *et al.*, 1990).

Another contrasting result was the total negative and positive effects of N in manure on the concentration of total N and ammonium in soil, respectively. Ammonium is commonly associated with human activities, as intensive agriculture and livestock produce significant amounts of this N source (Fig. 2; Anderson *et al.*, 2003; Clarisse *et al.*, 2009; Canfield *et al.*, 2010). Our results suggest that at least a part of the ammonium present in dryland soils may come from human-derived activities. Overall, the observed increase in soil ammonium concentrations with increased human activities may increase the potential of N to cross ecosystem boundaries by volatilization of ammonia or through conversion of ammonium to nitrate followed by leaching from soil. These are common phenomena in drylands (Schlesinger *et al.*, 1990; Robertson & Groffman, 2007) and may cause eutrophication and reduce water quality (Schlesinger *et al.*, 1990; Schlesinger & Harley, 1992; Robertson & Groffman, 2007; Ravishankara *et al.*, 2009). As processes such as nitrification usually require small amounts of water (Schwinning & Sala, 2004; Delgado-Baquerizo *et al.*, 2013c), the accumulation of ammonium in the less arid drylands may quickly promote its conversion to nitrate, even after small rainfall events (Schwinning & Sala, 2004). Our study supports this, as we observed an increase in the potential net nitrification rate in our soils with increasing ammonium ($P < 0.001$; Fig. S2). However, the 'real' rates at which these processes occur in nature do not necessary need to match our potential rates. The overall dominance of inorganic forms of N resulting from increasing human impacts may enhance nitrification and denitrification rates in drylands (e.g. releasing N_2O; Schlesinger, 2009; Canfield *et al.*, 2010), potentially enhancing the emission of greenhouse gases from these ecosystems.

CONCLUSIONS

Our findings provide evidence that human impacts promote the accumulation of N in dryland soils world-wide, but these effects are offset by increases in aridity. We also found that the effects of aridity and human impacts are spatially disconnected in drylands, favouring N losses and accumulation in the most and less arid ecosystems, respectively. Our analyses indicate that both increasing aridity and human impacts could potentially enhance inorganic control of the N cycle in drylands soils. This increase in dominance of inorganic N in dryland soils may have negative effects on key ecosystem functions (e.g. nutrient cycling) and services (e.g. air and water quality) at the global scale, and may enhance the emission of important greenhouse gases such as N_2O.

ACKNOWLEDGEMENTS

This research is supported by the European Research Council (ERC) under the European Community's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement no. 242658 (BIOCOM), and by the Ministry of Science and Innovation of the Spanish Government, grant no. CGL2010-21381. CYTED funded networking activities (EPES, Acción 407AC0323). S.G. was funded by CONICYT/FONDAP/15110009.

REFERENCES

Allen, S.E., Grimshaw, H.M. & Rowland, A.P. (1986) *Chemical analysis. Methods in plant ecology*. Blackwell Scientific, Oxford.

Anderson, N., Strader, R. & Davidson, C. (2003) Airborne reduced nitrogen ammonia emissions from agriculture and other sources. *Environment International*, **29**, 277–289.

Aznar-Sánchez, J.A. & Galdeano-Gómez, E. (2011) Territory, cluster and competitiveness of the intensive horticulture in Almería, Spain. *Open Geography Journal*, **4**, 103–114.

Bai, E., Li, S., Xu, W., Li, W., Dai, W. & Jiang, P. (2013) A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*, **199**, 441–451.

Baker, L.A., Hope, D., Xu, Y., Edmonds, J., Lauver, L. (2001). Nitrogen Balance for the Central Arizona–Phoenix (CAP) *Ecosystem. Ecosystems* **4**, 582–602.

Beelen, R., Hoek G., Vienneau, D. *et al.* (2013) Development of NO_2 and NO_x land use regression models for estimating air pollution exposure in 36 study areas in Europe – the ESCAPE project. *Atmospheric Environment*, **72**, 10–23.

Bistinas, I., Harrison, S.P., Prentice, I.C., Pereira, J.M.C. (2014). Causal relationships versus emergent patterns in the global controls of fire frequency. *Biogeosciences*, **11**, 5087–5101

Canfield, D.E., Glazer, A.N. & Falkowski, P.G. (2010) The evolution and future of Earth's nitrogen cycle. *Science*, **330**, 192–196.

Chen, H., Zhu, Q., Peng, C. *et al.* (2013) The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biology*, **19**, 2940–2955.

Clarisse, L., Clerbaux, C., Dentener, F., Hurtmans, D. & Coheur, P.-F. (2009) Global ammonia distribution derived from infrared satellite observations. *Nature Geoscience*, **2**, 479–483.

Compton, J.E., Harrison, J.A., Dennis, R.L., Greaver, T.L., Hill, B.H., Jordan, S.J., Walker, H. & Campbell, H.V. (2011) Ecosystem services altered by human changes in the nitrogen cycle, a new perspective for US decision making. *Ecology Letters*, **14**, 804–815.

Cornell, S.E. (2011) Atmospheric nitrogen deposition. Revisiting the question of the importance of the organic component. *Environmental Pollution*, **159**, 2214–2222.

Cui, S., Shi, Y., Groffman, P.M., Schlesinger, W.H. & Zhu, YG. (2013) Centennial-scale analysis of the creation and fate of reactive nitrogen in China 1910–2010. *Proceedings of the National Academy of Sciences USA*, **110**, 2052–2057.

Delgado-Baquerizo, M. & Gallardo, A. (2011) Depolymerization and mineralization rates at 12 Mediterranean sites with varying soil N availability. A test for the Schimel Bennett model. *Soil Biology and Biochemistry*, **43**, 693–696.

Delgado-Baquerizo, M., Maestre, F.T. & Gallardo, A. (2013a) Decoupling of nutrient cycles as a function of aridity in global dryland soils. *Nature*, **502**, 672–676.

Delgado-Baquerizo, M., Morillas, L., Maestre, F.T. & Gallardo, A. (2013b) Biocrusts control the nitrogen dynamics and microbial functional diversity of semi-arid soils in response to nutrient additions. *Plant and Soil*, **372**, 643–654.

Delgado-Baquerizo, M., Maestre, F.T., Rodriguez, J.G.P. & Gallardo, A. (2013c) Biological soil crusts promote N accumulation in response to dew events in dryland soils. *Soil Biology and Biochemistry*, **62**, 22–27.

Dentener, F., Drevet, J., Lamarque, J.F. *et al.* (2006) Nitrogen and sulfur deposition on regional and global scales. A multimodel evaluation. *Global Biogeochemical Cycles*, **20**, GB4003.

Drechsel, P. *et al.* (2001) Population density, soil nutrient depletion, and economic growth in sub-Saharan Africa. *Ecological Economics*, **38**, 251–258.

Durán, J., Delgado-Baquerizo, M., Rodríguez, A., Covelo, F. & Gallardo, A. (2012) Ionic exchange membranes (IEMs): a good indicator of soil inorganic N production. *Soil Biology and Biochemistry*, **57**, 964–968.

Feng, S. & Fu, Q. (2013) Expansion of global drylands under a warming climate. *Atmospheric Chemistry and Physics*, **13**, 10081–10094.

Gadsdon, S.R. & Power, S.A. (2009) Quantifying local traffic contributions to NO_2 and NH_3 concentrations in natural habitats. *Environmental Pollution*, **157**, 2845–2852.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Trends, questions, and potential solutions transformation. *Science*, **320**, 889–892.

Gilbert, N.L., Goldberg, M.S. Brook, J.R. & Jerrett, M. (2007) The influence of highway traffic on ambient nitrogen dioxide concentrations beyond the immediate vicinity of highways. *Atmospheric Environment*, **41**, 2670–2673.

Gill, J.A., Sutherland, W.J. & Watkinson, A.R. (1996) A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, **33**, 786–792.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.M., Pretty, J., Robinson, S., Thomas, S.M. & Toulmin, C. (2010) Food security, the challenge of feeding 9 billion people. *Science*, **327**, 812–818.

Grace, J.B. (2006) *Structural equation modeling and natural systems*. Cambridge University Press, New York.

Gruber, N. & Galloway, J.N. (2008) An Earth-system perspective of the global nitrogen cycle. *Nature*, **451**, 293–296.

Hall, S.J., Sponseller, R.A., Grimm, N.B., Huber, D., Kaye, J.P., Clark, C. & Collins, S. (2011) Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. *Ecological Applications*, **21**, 640–660.

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.

Jones, D.L. & Willett, V.B. (2006) Experimental evaluation of methods to quantify dissolved organic nitrogen DON and dissolved organic carbon DOC in soil. *Soil Biology and Biochemistry*, **38**, 991–999.

Kane, K., Tuccillo, J., York, A.M., Gentile, L. & Ouyang, Y. (2014) A spatio-temporal view of historical growth in downtown Phoenix, Arizona. *Landscape and Urban Planning*, **121**, 70–80.

Kettler, T.A., Doran, J.W. & Gilbert, T.L. (2001) Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science Society of America Journal*, **65**, 849–852.

Last of the Wild Data (2005) *Version 2 LWP-2: global human influence index (HII) and human footprint index*. Available at: http://sedac.ciesin.columbia.edu/data/collection/wildareas-v2/sets/browse.

Liu, J., You, L., Amini, M., Obersteiner, M., Herrero, M., Zehnder, A.J. & Yang, H. (2010) A high-resolution assessment on global nitrogen flows in cropland. *Proceedings of the National Academy of Sciences USA*, **107**, 8035–8040.

Maestre, F.T., Escolar, C., Ladrón de Guevara, M., Quero, J.L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B. & Gallardo, A. (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Global Change Biology*, **19**, 3835–3847.

Maestre, F.T., Quero, J.L., Gotelli, N.J. *et al.* (2012) Plant species richness ecosystem multifunctionality in global drylands. *Science*, **335**, 214–218.

Mainguet, M. (1999) *Aridity, droughts and human development*. Springer, New York.

MEA (2005) *Ecosystems and human well-being: desertification synthesis*. World Resources Institute, Washington, DC.

OECD/FAO (2011) *OECD-FAO agricultural outlook 2011–2020*. OECD Publishing and FAO, Paris. http://dx.doi.org/10.1787/agr_outlook-2011-en.

Potter, P., Ramankutty, N., Bennett, E.M. & Donner, S.D. (2011) *Global fertilizer and manure, version 1: nitrogen fertilizer application*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY. Available at: http://sedac.ciesin.columbia.edu/data/set/ferman-v1-nitrogen-fertilizer-application.

Ravishankara, A.R., Daniel, J.S. & Portmann, R.W. (2009) Nitrous oxide N_2O. The dominant ozone-depleting substance emitted in the 21st century. *Science*, **326**, 123–125.

Reynolds, J.F., Smith, D.M., Lambin, E.F. *et al.* (2007) Global desertification. Building a science for dryland development. *Science*, **316**, 847–851.

Robertson, G.P. & Groffman, P. (2007) *Soil microbiology, biochemistry, and ecology*. Springer, New York.

Schermelleh-Engel, K., Moosbrugger, K.H. & Müller, H. (2003) Evaluating the fit of structural equation models, tests of significance descriptive goodness-of-fit measures. *Methods of Psychological Research Online*, **8**, 23–74.

Schimel, J.P. & Bennett, J. (2004) Nitrogen mineralization, challenges of a changing paradigm. *Ecology*, **85**, 591–602.

Schlesinger, W.H. (2009) On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of Sciences USA*, **106**, 203–208.

Schlesinger, W.H. & Bernhardt, E.S. (2013) *Biogeochemistry, an analysis of global change*. Academic Press, San Diego, CA.

Schlesinger, W.H. & Harley, P.C. (1992) A global budget for atmospheric NH_3. *Biogeochemistry*, **15**, 191–211.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043–1048.

Schwinning, S. & Sala, O.E. (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, **141**, 211–220.

Seagle, S.W., McNaughton, S.J. & Ruess, R.W. (1992) Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. *Ecology*, **73**, 1105–1123.

Sims, G.K., Ellsworth, T.R. & Mulvaney, R.L. (1995) Microscale determination of inorganic nitrogen in water and soil extracts. *Communications in Soil Science and Plant Analysis*, **26**, 303–316.

Sollins, P., Glassman, C., Paul, E.A., Swantston, C., Lajtha, K., Heil, J.W. & Ellikott, E.T. (1999) *Soil carbon and nitrogen: pools and fraction. Standard soil methods for long-term ecological research*, pp. 89–105. Oxford University Press, Oxford.

Thomas, A.D., Hoon, S.R. & Dougill, A.J. (2011) Soil respiration at five sites along the Kalahari Transect: effects of temperature, precipitation pulses and biological soil crust cover. *Geoderma*, **167–168**, 284–294.

UNEP (1992) *United Nations Environment Programme world atlas of desertification*. Edward Arnold, London.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D.G. (1997) Human alteration of the global nitrogen cycle, sources and consequences. *Ecological Applications*, **7**, 737–750.

Warren, C.R. (2009) Does nitrogen concentration affect relative uptake rates of nitrate, ammonium, and glycine? *Journal of Plant Nutrition and Soil Science*, **172**, 224–229.

Whitford, W.G. (2002) *Ecology of desert systems*. Academic Press, San Diego, CA.

World Bank (2008) *World development report, agriculture for development*. World Bank, Washington, DC.

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.

Zornoza, R., Guerrero, C., Mataix-Solera, J., Arcenegui, V., García-Orenes, F. & Mataix-Beneyto J. (2006) Assessing air-drying and rewetting pre-treatment effect on some soil enzyme activities under Mediterranean conditions. *Soil Biology and Biochemistry*, **38**, 2125–2134.

Zornoza, R., Mataix-Solera, J., Guerrero, C., Arceneguia, V. & Mataix-Beneyto, J. (2009) Storage effects on biochemical properties of air-dried soil samples from southeastern Spain. *Arid Land Research and Management*, **23**, 213–222.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 A priori generic structural equation model (SEM) used in this study. Further explanation on the relationship between the variables included in this model can be found in Supplementary Methods S1.

Figure S2 Quadratic relationship between ammonium concentration and the potential net nitrification rate in the studied soils.

Table S1 Information about the population data used to estimate human impacts at our study sites.

Table S2 Correlation coefficients between the surrogates of human impacts evaluated in this study.

Supplementary Methods S1 Rationale for the variables included in our structural equation model.

BIOSKETCH

Manuel Delgado-Baquerizo is a soil ecologist with a wide range of interest in global change ecology, biological soil crusts, biogeochemistry, microbial ecology and ecosystem ecology in general (dryland ecology in particular). His current interest is in understanding how global change will affect soil functionality and stability in terrestrial ecosystems.

Editor: Thomas Hickler