



Tesis doctoral

Umbrales climáticos en la estructura y funcionamiento de las zonas áridas a escala global

Autor:

Miguel Berdugo Vega

Directores:

Dr. Fernando T. Maestre Gil

Dr. Santiago Soliveres Codina

Dra. Sonia Kéfi

Departamento de Biología, geología, física y química inorgánica

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Dr. Fernando T. Maestre Gil, profesor titular del departamento de biología, geología, física y química inorgánica de la Universidad Rey Juan carlos; el Dr. Santiago Soliveres Codina, investigador del departamento de de la Universidad de Berna; y la doctora Sonia Kéfi, investigadora en el Institut des Sciences de l'Evolution de Montpellier (Centre National de la Recherche Scientifique, France),

CERTIFICAN

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral “Umbrales climáticos en la estructura y funcionamiento de las zonas áridas a escala global”, son aptos para ser presentados por el licenciado Miguel Berdugo Vega ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en el Programa de Doctorado de Conservación de Recursos Naturales por la Universidad Rey Juan Carlos de Madrid.

Vº Bº Director de Tesis

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Vº Bº Director de Tesis

Sonia Kéfi

Fernando T. Maestre Gil

Santiago Soliveres Codina

A quienes resuenan conmigo

¿Propiedad emergente, dices?, Es fácil:
 $1 + 1 > 2$

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RESUMEN



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INTRODUCCIÓN

Definición de zonas áridas y del concepto de umbral

Las zonas áridas (del inglés, drylands) comprenden aquellos lugares del mundo donde el coeficiente entre precipitación y evapotranspiración es menor que 0,65 (i.e., llueve menos de un 35% de la demanda evaporativa, por lo tanto son aquellos lugares donde existe un déficit de agua crónico e histórico, Middleton and Thomas, 1992; Whitford, 2002). Dependiendo del valor de su índice de aridez (el coeficiente precipitación: evapotranspiración), las zonas áridas son clasificadas en hiperáridas, áridas, semiáridas y seco-subhúmedas (índice de aridez <0,05, hasta 0,2, hasta 0,5 y hasta 0,65 respectivamente). Estos sitios representan más del 45% de las tierras emergidas de nuestro planeta (5,9%, 14,2%,16,4% y 9% respectivamente para sistemas hiperáridos, áridos, semiáridos y seco-subhúmedos; Právālie, 2016), son el bioma más grande del mundo y constituyen el hogar del 37% de la población mundial (Reynolds et al., 2007). El modo de vida de las personas que habitan en estos lugares, que son dominantes entre los países en vías de desarrollo, depende en gran medida de la capacidad de los ecosistemas para proveer servicios tales como agua o forraje (Millenium Ecosystem Assessment 2005). Es por ello que el estudio de los ecosistemas, y en particular de las relaciones entre sus elementos bióticos y la capacidad que tienen de proveer de servicios a la población, juega un papel especialmente fundamental para garantizar la sostenibilidad de las zonas áridas.

Los ecosistemas de las zonas áridas están restringidos a la capacidad de sus organismos para adaptarse y sobrevivir al déficit de agua. Son sistemas complejos, cuya dinámica y funcionamiento depende en gran medida de procesos de retroalimentación positiva desempeñados principalmente por plantas que los ocupan. Por ejemplo, algunas plantas en estos sistemas (las llamadas "plantas nodriza") mejoran las condiciones microclimáticas en su entorno más inmediato, incrementando sustancialmente tanto el reclutamiento como el crecimiento de otras plantas que se encuentran en sus inmediaciones (Maestre et al. 2001, 2003b, Cavieres and Badano 2009). El efecto del cambio climático es muy probable que se amplifique a través de estos procesos de retroalimentación (por ejemplo,

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mediante extinciones en cascada cuando las plantas nodriza no pueden soportar el cambio ambiental, (Xu et al. 2015b, Kéfi et al. 2016), y por tanto las especies que dependen de ellas desaparecen también. Por tanto, las respuestas que se esperan en los ecosistemas de zonas áridas ante el cambio climático es muy probable que se den de forma no lineal o incluso abrupta (Groffman et al. 2006). En este contexto, esta tesis pretende investigar la existencia de umbrales de cambio con la aridez en los ecosistemas de las zonas áridas. Los umbrales de cambio (“thresholds” en inglés) son puntos a partir de los cuales incrementos pequeños del factor externo (p. ej., clima, como lo es la aridez en nuestro caso) pueden producir alteraciones abruptas en alguno o varios de los componentes del ecosistema (Groffman et al. 2006). Un ejemplo de ello es la desertificación, que produce caídas de la funcionalidad y producción del ecosistema abruptas en respuesta a incrementos de pastoreo o al endurecimiento de las condiciones climáticas (Schlesinger et al. 1990, Reynolds et al. 2007, Verwijmeren et al. 2013).

La investigación de umbrales de cambio en ecología no es un tema nuevo, y ha sido abordado por múltiples investigadores. Sin embargo, hay una serie de deficiencias en su estudio. Por ejemplo, no existe una utilización homogénea del término "umbral". A veces umbral se refiere a valores específicos en una variable de interés (p. ej., la supervivencia de una especie baja más del 50%, ver por ejemplo Ficetola and Denoël, 2009), y a veces a cambios bruscos no lineales o catastróficos (p. ej., Tremblay et al., 2006). Los cambios catastróficos son cambios producidos en un sistema debido al hecho de que exhibe estados estables alternativos en su dinámica (Zeeman 1977; Strogatz 2014, p. ej., desertificación o matorralización, ver Schlesinger et al. 1990, Suding et al. 2004, D’Odorico et al. 2012). Por ello, para un determinado valor de la variable que describe las condiciones del sistema (p. ej., intensidad de pastoreo en procesos como la desertificación), el ecosistema puede estar en un estado u otro dependiendo de las condiciones iniciales de las que parte (p. ej., un ecosistema funcional o degradado). Estos últimos cambios tienen gran trascendencia en ecología, dado que implican que, si un ecosistema cambia de un estado funcional a otro que no lo es, para recuperar su estado funcional puede no bastar con que se recuperen las condiciones anteriores a producirse el cambio (Scheffer et al. 2001). Además, los umbrales de cambio en ecosistemas pueden involucrar alteraciones en varias

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características del mismo. Pese a ello, los estudios desarrollados a día de hoy se han centrado en sólo unas pocas características del ecosistema (p. ej., cobertura total de la vegetación, Rietkerk and de Koppel 1997; Kéfi et al. 2007b; Scheffer et al. 2012), desatendiendo otras que también son importantes para la estructura y el funcionamiento de los ecosistemas (p. ej., cambios en la composición de especies, en la importancia de interacciones bióticas o en la fertilidad del suelo). Por último, los umbrales de cambio se han estudiado mediante aproximaciones teóricas predominantemente (Scheffer et al. 2001, Kéfi et al. 2007b), mientras que los estudios en ecosistemas reales y datos de campo son mucho más escasos. Como consecuencia de éstas limitaciones, la mayoría de los estudios sobre umbrales de desertificación no incluyen muchos de los procesos ecosistémicos que se pueden ver afectados por este proceso, como las reservas de carbono en el suelo, la capacidad del suelo para capturar agua, o las tasas de transformación y reciclaje de nutrientes. Los pocos estudios que incluyen dichas variables funcionales sugieren la existencia de umbrales de funcionamiento ecosistémico a través de gradientes de aridez. Por ejemplo, se han encontrado umbrales en el reciclado de nitrógeno alrededor de valores de aridez ~ 0.3 (Wang et al. 2014), que sugieren un cambio importante y brusco en la forma en que ocurre la mineralización del nitrógeno en el suelo. Estos cambios bruscos pueden afectar a la vegetación, que a su vez afecta a la provisión de nutrientes de origen biótico al suelo, desembocando en el desacople de nutrientes como el nitrógeno y el fósforo (Delgado-Baquerizo et al. 2013). No se ha estudiado, sin embargo, el hecho de que estos desacoples pudieran generar patrones con estados alternativos estables en la fertilidad del suelo. A este respecto, un número creciente de estudios ha demostrado que el funcionamiento ecosistémico se haya influenciado por la composición de las comunidades vegetales (Lavorel and Garnier 2002, Díaz et al. 2007, Conti and Díaz 2013, Valencia et al. 2015). Este efecto es producido por los rasgos funcionales que exhiben estas comunidades, su diversidad y el modo diferencial en que afectan a funciones como el reciclado de nutrientes o la producción del ecosistema (Lavorel and Garnier 2002, Conti and Díaz 2013, Valencia et al. 2015). Es por ello que cambios en la composición, diversidad o características de las especies que conforman una comunidad ecológica pueden afectar de manera no lineal a su funcionamiento.

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La detección de umbrales en la composición de especies a lo largo de gradientes de aridez es infrecuente a escala global. No obstante, algunos estudios sugieren cambios en los síndromes de rasgos funcionales a lo largo de gradientes regionales de aridez (Gross et al. 2013, Le Bagousse-Pinguet et al. 2017a), mostrando una dominancia de especies evasoras del estrés (del inglés “stress avoidant”) en ambientes de extrema aridez (entre semiárido y árido), cuyos rasgos funcionales son muy distintos de los exhibidos por especies tolerantes del estrés (Poorter et al. 2009, Gross et al. 2013, Maire et al. 2015). Otros estudios han identificado cambios bruscos en la diversidad beta (cambios en la identidad de las especies entre un sitio y otro de la misma región) a escala global (Ulrich et al. 2014). Estos cambios consisten en reducciones drásticas de la diversidad beta a partir de precipitaciones menores a 178 mm, sugiriendo que sólo unas pocas especies son capaces de colonizar de forma eficiente sitios con este nivel de aridez. Aunque es probable que estos cambios se deban a una modificación en la estrategia de las especies para afrontar las duras condiciones de las zonas áridas más extremas, no se han asociado de momento estos cambios a la capacidad de las especies para medrar frente a la aridez. Tampoco está claro si este cambio composicional afecta a la manera en que el ecosistema se estructura dinámica y funcionalmente. Debido a que existe una dependencia entre la capacidad de las especies de adaptarse al clima en que viven y la manera en que interactúan unas con otras (p. ej., las especies más adaptadas no suelen necesitar ser facilitadas para medrar, Choler et al., 2001; Liancourt et al., 2005; Gross et al., 2010; Soliveres et al., 2012), es probable que cambios en la composición de comunidades afecten a la relación que establecen unas especies con otras. Esto puede amplificar cambios composicionales dado que las relaciones planta-planta en los ecosistemas áridos influyen de modo importante en qué especies son capaces de sobrevivir, así como en su abundancia (Liancourt et al. 2005, Cavieres and Badano 2009, Gross et al. 2013, Soliveres et al. 2015a).

Para entender cómo cambios en la composición de especies pueden llegar a ocurrir en comunidades vegetales es necesario entender cómo éstas se ensamblan. Como en muchos otros ecosistemas, en las zonas áridas hay dos moduladores principales de este proceso, un filtrado abiótico, que decide las especies que pueden subsistir en un rango climático dado, y las

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interacciones bióticas (p. ej., facilitación y competición) que determinan la composición final (Keddy 1992, Götzenberger et al. 2012). Sin embargo, se desconoce la importancia relativa de estos factores a lo largo de gradientes de aridez. En particular, las interacciones planta-planta constituyen un filtro clave durante el ensamblaje de comunidades. Sin embargo, no existe consenso a día de hoy sobre cómo varía su importancia a lo largo de gradientes de aridez. Por ejemplo, se espera que la intensidad de interacciones positivas entre plantas (facilitación) aumente conforme incrementa la aridez (Bertness and Callaway 1994, Callaway et al. 2002). Sin embargo, se han hipotetizado también patrones unimodales, que sugieren que esta intensidad decrece en ambientes muy extremos (Hacker and Gaines 1997, Michalet et al. 2006, Holmgren and Scheffer 2010), y también que depende casi exclusivamente del tipo de especies involucradas en la interacción (Liancourt et al. 2005, Soliveres et al. 2012, 2014a). Los cambios en las interacciones entre plantas a lo largo de gradientes ambientales son importantes para predecir pérdidas de diversidad en el futuro, pero también para entender el papel de éstas interacciones en la formación de manchas de vegetación y el funcionamiento ecosistémico. Sin embargo, las distintas hipótesis que predicen cambios en las interacciones planta-planta a lo largo de gradientes ambientales se han evaluado sin tratar de controlar las interrelaciones existentes entre los filtro bióticos y abióticos que interactúan en el ensamblaje de comunidades (Brooker et al. 2008, Soliveres et al. 2015b). Por tanto, carecemos de aproximaciones más inclusivas que evalúen de forma completa la importancia relativa de los factores que afectan a éstos cambios.

Aparte de a través de la composición funcional de las comunidades y de sus efectos sobre la riqueza, las interacciones planta-planta pueden afectar a otros atributos importantes de los ecosistemas, como el patrón espacial de la vegetación (Manor and Shnerb 2008a, Meron 2015). En las zonas áridas, la vegetación se haya organizada en forma de manchas discretas dispersas en una matriz de suelo desnudo sin vegetación vascular perenne (Tongway et al. 2001, ver Figura 1). La dinámica y evolución de estas manchas han sido objeto de estudio debido a que pueden llegar a formar patrones muy característicos como consecuencia a la auto-organización de las plantas (p. ej., a través de las interacciones que ocurren entre ellas). En particular, hay

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muchos estudios teóricos que vinculan las interacciones planta-planta a distintos tipos de patrones espaciales, asociando la agregación y segregación de las manchas de vegetación con interacciones positivas (Kéfi et al. 2007b, Scanlon et al. 2007) y negativas (Manor and Shnerb 2008a, Xu et al. 2015a), respectivamente. Sin embargo, hay pocas evidencias empíricas acerca del papel que cumplen las interacciones planta-planta en el patrón espacial del ecosistema (ver, no obstante, Xu et al., 2015). De manera relevante, se han hipotetizado vínculos claros entre el cambio en la distribución espacial de la vegetación y umbrales entre sistemas fértiles y desertificados (Kéfi et al. 2007a, 2014). Estos estudios sugieren que la distribución de frecuencias en los tamaños de mancha de vegetación en el ecosistema cambia de manera evidente justo antes de producirse un cambio abrupto. Sin embargo, las evidencias empíricas al respecto contradicen estas hipótesis en cuanto a los cambios en el funcionamiento ecosistémico están más relacionados con cambios en la cobertura vegetal total que a cambios en los patrones espaciales (Maestre and Escudero 2009, Pueyo et al. 2012, Bestelmeyer et al. 2013). No obstante, no existen a día de hoy estudios desarrollados a escalas globales y regionales que comprendan un abanico de condiciones representativo de zonas áridas (ver ejemplos a escala local en Kéfi et al. 2007a; Lin et al. 2010; Moreno de las Heras et al. 2011). Estos estudios podrían llevar a evaluar la importancia funcional de los patrones espaciales de la vegetación con una mayor precisión, permitiendo establecer bajo qué condiciones se dan ciertos patrones espaciales así como el carácter universal de ciertas de sus propiedades.



Figura 1.1. Patrón espacial de las zonas áridas.

Fotografía aérea del patrón espacial de la vegetación tomada con un dron en un espartal en el mar de Ontígola (España).

IMPORTANCIA Y OBJETIVOS

El estudio de umbrales de cambio en las zonas áridas debido a aumentos de la aridez es de vital trascendencia para predecir y mitigar los efectos del cambio climático tanto en estos ecosistemas como en los servicios que éstos proveen y de los que una gran parte de su población depende (Millenium Ecosystem Assessment 2005). En esta tesis estudio umbrales de cambio utilizando una serie de técnicas que permiten evaluar tendencias no lineales en los distintos componentes estructurales del ecosistema, así como en su funcionamiento, utilizando para ello una base de datos global de zonas áridas (BIOCOM, ver Maestre et al., 2012). Es el objetivo primordial de esta tesis centrarse en la localización y descripción de estos umbrales de cambio, así como el de comprender las relaciones existentes entre los distintos componentes ecosistémicos (*sensu* Tomimatsu et al., 2013: patrón espacial, composición de la comunidad y red de interacciones) y el funcionamiento de los ecosistemas cuando estos umbrales se producen. Para ello, esta tesis se organiza en cuatro capítulos cuyos objetivos específicos son:

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- Capítulo 1: Determinar la tipología de los patrones espaciales en la vegetación de las zonas áridas a una escala global, así como los factores que modulan su generación. Distintos tipos de patrón espacial podrían indicar umbrales de cambio en los mismos con incrementos de aridez, por tanto, en este capítulo se sientan las bases para poder evaluar umbrales de cambio en los patrones espaciales de la vegetación. En este capítulo encontramos que existen dos tipos de patrones espaciales en zonas áridas atendiendo a su capacidad de formar agregados de manchas de vegetación grandes por facilitación, y que su existencia y morfología están determinados por distintos factores dependiendo del tipo de patrón espacial considerado.
- Capítulo 2: Relacionar los distintos tipos de patrón espacial de la vegetación encontrados en el Capítulo 1 con la multifuncionalidad (habilidad del ecosistema de proveer múltiples funciones simultáneamente), comparando su capacidad de explicarla con la de la cobertura de la vegetación. En este capítulo se encontraron umbrales de cambio en la funcionalidad ecosistémica y se comprobó su asociación con umbrales de cambio en el patrón espacial. Concluimos que existen cambios abruptos en la funcionalidad que son identificados con umbrales de cambio en el patrón espacial, pero no con la cobertura de la vegetación.
- Capítulo 3: Investigar posibles cambios en la importancia de las interacciones planta-planta como factores de ensamblaje de comunidades a nivel global, con especial énfasis en averiguar la relación de estos patrones con la habilidad de las plantas para adaptarse a la aridez. En este capítulo encontramos que cambios en la capacidad de adaptación de las especies a lo largo de un gradiente de aridez determinan cambios cualitativos en la importancia de las interacciones planta-planta como factores de ensamblaje de las comunidades vegetales. Como consecuencia de ello, la importancia de la facilitación como factor de ensamblaje de comunidades decrece conforme aumenta la aridez, y aumenta la de la competencia.
- Capítulo 4: Relacionar cambios composicionales en la comunidad con patrones espaciales y su asociación con la multifuncionalidad. En este capítulo se investiga la relación entre la existencia de umbrales en la composición y patrón espacial de la vegetación y en la funcionalidad

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del ecosistema. En este capítulo se encontró que los cambios composicionales en las comunidades influyen de modo importante en los cambios en el patrón espacial de la vegetación y en la funcionalidad del ecosistema. Estos cambios parecen estar asociados a un cambio de síndromes de rasgos funcionales.

- Discusión general: aquí discuto y sintetizo los nuevos aportes proporcionados por esta tesis doctoral, otorgando un enfoque holístico de la existencia de umbrales climáticos en los ecosistemas de zonas áridas a nivel global.

METODOLOGÍA

Para el desarrollo de esta tesis se cuenta con la base de datos global de zonas áridas de Maestre et al. (2012), que incluye información acerca de la estructura (especies y abundancia, cobertura total de plantas perennes) y funcionamiento (medidas de funciones de la fertilidad del suelo en hasta 16 variables relacionadas con los ciclos del carbono, nitrógeno y fósforo). Esta base de datos contiene información de ecosistemas de 19 países repartidos por todos los continentes excepto la Antártida, que abarcan un amplio rango de condiciones abióticas (clima, elevación, tipos de suelo y topología) y bióticas (tipos de vegetación, cobertura total de vegetación y riqueza de especies), y es ideal para el estudio de umbrales de cambio debido también a la gran cantidad de sitios muestreados ($N = 236$).

Además de la información ya contenida en esta base de datos, en esta tesis se obtuvo información acerca de los patrones espaciales de los ecosistemas muestreados utilizando técnicas de procesamiento y clasificación de imágenes por satélite (Solomon and Breckon 2011). Estas técnicas permitieron extraer el tamaño de manchas de vegetación del ecosistema de estudio. Con ellos se ajustaron las llamadas distribuciones de tamaño de manchas (“patch-size distributions” en inglés), que describen la frecuencia de los distintos tamaños de manchas de vegetación (Kéfi et al. 2007a, Scanlon et al. 2007) de acuerdo a ecuaciones potenciales (del inglés “power law”, ver (Clauset et al. 2009)), arrojando información acerca de diversas características espaciales del ecosistema (p. ej., creación de manchas grandes,

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tamaño medio de las manchas de vegetación y tipo de distribución de frecuencias de los tamaños de mancha).

También se han obtenido en esta tesis información acerca de los nichos climáticos de las especies muestreadas. Para hacer esto, se aplicaron modelos de distribución de especies (en inglés “Species Distribution Models”, SDMs, Elith & Leathwick, 2009) en todas las especies de la base de datos global utilizada. Esto permite obtener estimas del grado de adaptación de las especies a las condiciones climáticas en las que se encuentran (Soberon and Townsend Peterson 2005, Soberón 2007), además de información sobre compromisos entre el grado de adaptación y las condiciones ambientales (rango) en que se mueven estas especies (*i.e.*, especialización de las especies, ver Devictor et al. 2010). Este tipo de información es de gran relevancia, por ejemplo, para ser considerada como covariable a la hora de estudiar la importancia de las interacciones bióticas para la estructura del ecosistema, sin embargo es generalmente pasada por alto en estudios de comunidad sobre interacciones planta-planta.

En esta tesis se usaron herramientas estadísticas que permiten la identificación de estados alternativos utilizando datos empíricos (ver Livina and Lenton, 2007). También se investigaron las interacciones entre diversas variables en modelos generales lineales para poder establecer el cambio de la importancia de las mismas como predictores estadísticos a lo largo de gradientes de aridez. Dichos gradientes de aridez están descritos como 1 – índice de aridez (calculado este último como el cociente entre precipitación y evapotranspiración, ver (Middleton and Thomas 1992)). En todos los capítulos de la tesis, la aridez ha sido calculada del mismo modo, y constituye el predictor fundamental de los cambios en los distintos componentes del ecosistema evaluados.

AFILIACIÓN DE LOS COAUTORES

Fernando T. Maestre: Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain

Santiago Soliveres: Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

Nicolas Gross : CNRS – Université La Rochelle (UMR 7372), Centre d'étude Biologique de Chizé, Villiers-en-Bois, France.

Yoann Le Bagousse-Pinguet: Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain

Sonia Kéfi: Institut des Sciences de l'Evolution, BioDICée team, Université de Montpellier, CNRS, IRD, EPHE, CC 065, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France.

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INTRODUCTION



Introduction

DRYLANDS AS COMPLEX SYSTEMS

Drylands are water-limited ecosystems occupying areas where the aridity index (calculated as the quotient between annual precipitation and potential evapotranspiration) is lower than 0.65 (Middleton and Thomas 1992). Depending on the value of their aridity index, drylands are categorized in hyperarid, arid, semi-arid and dry-subhumid systems (aridity index <0.05, up to 0.2, up to 0.5 and up to 0.65, respectively). In total, these ecosystems cover ~45% of the Earth's surface (5.9%, 14.2%, 16.4% and 9%, respectively, for hyperarid, arid, semi-arid and dry-subhumid systems, Právělie, 2016), making it the largest terrestrial biome on Earth. These areas include 28.71% of South America, 31.7% of North America and Central America, 86.4% of Oceania, 74.99% of Africa, 50.9% of Asia and 17.5% of Europe (Figure 2.1, Právělie 2016).

About 35.5% of the total human population (over 2 billion people), in particular from developing countries (90% of total dryland inhabitants), live in drylands (Safriel and Adeel 2005). Importantly poverty is a common problem in most of the countries where drylands occur (about 50% of dryland inhabitants are estimated to be poor; Middleton and Sternberg 2013). Also, the proportion of dryland inhabitants who live in developing countries increases with aridity (100% of hyperarid ecosystems occur in developing countries). Land use in drylands is constrained by the productivity of these ecosystems and shifts from agriculture to grazing with aridity (from 34/47 [dry-subhumid] to 97/0.6 % [Hyper-arid] of the area for rangelands/cultured lands according to Millenium Ecosystem Assessment 2005). All these factors imply that the livelihoods of people living in drylands largely depend on the services provided by these ecosystems, which are strongly linked to the attributes of their biotic communities (Middleton and Sternberg 2013). For instance, changes in species richness and composition affect the rates, provision and variety of the ecosystems, particularly those related to water and forage provision (Millenium Ecosystem Assessment 2005, Maestre et al. 2012a, Bestelmeyer et al. 2015). Therefore, improving our understanding on how biotic factors modulate both the functioning and the provision of services by dryland ecosystems is of paramount importance to ensure the

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livelihood of people inhabiting them and thus the global sustainability of our planet.

Importantly, drylands are iconic examples of complex systems, due to the role of the feedbacks arising between vegetation, climate and soils as drivers of their structure and functioning (e.g., D'Odorico et al. 2007; Okin et al. 2009; Ravi et al. 2009). Dryland encompass a diverse mixture of ecosystems (e.g., grasslands, shrublands, savannah), which are typically structured by plant patches interspersed within a matrix devoid of plant vegetation (Aguiar and Sala 1999, Tongway et al. 2001). This entails important consequences for ecosystem structure and functioning. Vascular plants modify their environment by retaining resources and changing the micro-environmental conditions below their canopies (Niering et al. 1963, Aguiar and Sala 1999, Whitford 2002, Berdugo et al. 2014). Given the role of vegetated patches as sinks for resources, their spatial distribution creates a complex spatial heterogeneity through a process called self-organization, i.e., the process by which parts of the system interacts locally generating emerging properties at larger scales, such as spatial patterns of plant patches (Scanlon et al. 2007; Manor and Shnerb 2008a; Rietkerk and de Koppel 2008; Bowker and Maestre 2012; Meron 2015). Self-organization affects multiple ecosystem attributes and processes, including species diversity, community assembly, primary productivity, erosion, or rainfall infiltration (Aguiar and Sala 1999, Tongway et al. 2001, Maestre 2006, Mayor et al. 2008, Ludwig et al. 2013, Berdugo et al. 2014).

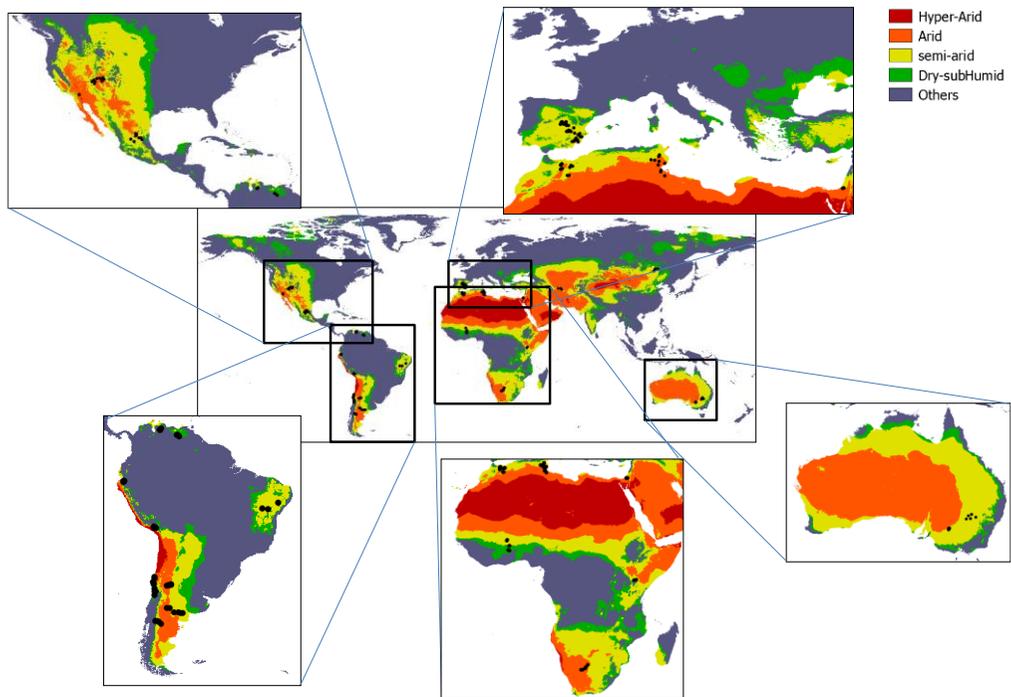


Figure 2.1. Drylands of the world.

Map of global drylands, with location of the sites used in this work (black dots). See Maestre et al. (2012a) and the methods chapter of this thesis for a full description of the study sites. Aridity information was extracted using maps from Zomer et al. (2008).

ENVIRONMENTAL THRESHOLDS IN DRYLANDS AND CLIMATE CHANGE

Feedbacks between climate, soil and vegetation not only determine the productivity and diversity of dryland plant communities (Aguar and Sala 1999, Ehrenfeld et al. 2005, D’Odorico et al. 2007, Laird and Schamp 2009, Soliveres and Maestre 2014), but also modulate the way in which dryland ecosystems face external disturbances (Folke et al. 2004, Suding et al. 2004, Maestre et al. 2010, Escolar et al. 2015). For instance, improvement in microclimate under plant canopies of adapted nurse plants may foster the recruitment of plants not adapted to the harsh environmental conditions of drylands (facilitation, Bertness and Callaway 1994; Valiente-Banuet et al. 2006; Brooker et al. 2008). This makes species response to environmental

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harshness highly dependent on whether nurses can cope with increases in abiotic stress, thus it may lead to amplifications of diversity loss with climate change. Also environmental amelioration improves the physiological status of plants under nurses (Maestre et al. 2003b), and plant-plant interactions may also create spatial arrangements that maximize water uptake (Aguiar and Sala 1999) or prevent soil erosion (Bautista et al. 2007). As a last example, it has been recently observed that plant communities exhibit plant trait distributions that maximize ecosystem functioning in global drylands (Gross et al. 2017). This is hypothesized to occur through density-dependence mechanisms, plant-plant interactions or niche stabilizing processes, being all these mechanisms related with self-organizing processes promoted by vegetation (MacArthur and Levins 1967, Levine and HilleRisLambers 2009, Gross et al. 2015). Thus, the dependence of ecosystems on the ability of plants to improve their own conditions creates a strong feedback that, if affected, may lead into abrupt changes of ecosystems (e.g., desertification by plant removal of grazers, see Schlesinger et al. 1990; D'Odorico et al. 2013).

Because of their complex dynamics, it is unlikely that drylands will respond proportionally to changes in environmental drivers. Nonlinear responses to external factors may be smooth, but they may also cause abrupt shifts in ecosystem properties. In this latter case, this means that there are certain levels of environmental factors around which ecosystems may be very sensitive to a further increase in this factor. These levels are called thresholds, which are defined as “the point in which there is an abrupt change in an ecosystem quality, property or phenomenon, or where small changes in an environmental driver produce large responses on the ecosystem” (Groffman *et al.* 2006, see Figure 2.2). The study of thresholds has a long history in ecology because of their implications for ecosystem management and restoration (Groffman et al. 2006, Suding and Hobbs 2009). Introduced in early 70s by a number of theoretical studies (Holling 1973, Noy-Meir 1975, May 1976), and popularized by authors such as Steven Carpenter (Folke et al. 2004) and Marten Scheffer (Scheffer et al. 2001), the concept of catastrophic shifts is one of the most famous examples of abrupt threshold in ecology and its implications (Figure 2.2.b). These shifts occur in ecosystems that exhibit several alternative stable states that co-occur for the same levels of external factors (e.g., environmental conditions). When environmental

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conditions overcome a threshold, they trigger a change in the state of the ecosystem that transforms the ecosystem profoundly and abruptly (van Nes et al. 2016, Figure 2.2.b.). Importantly, environmental changes promoting an abrupt transition from one state to another (let's call them state *a* and state *b*) are different from those that would reverse it (from state *b* to *a*). This phenomenon is known as hysteresis (Morris 2011) and causes that, provided that the threshold has been surpassed, degradation might still be persistent even if the factor promoting it ceases. Ecosystems have been shown to experience this type of transitions, for instance, in drylands as a response to environmental harshness or grazing intensity (Okin et al. 2009, D'Odorico et al. 2013, Bestelmeyer et al. 2015); or in shallow lakes due to eutrophication (Scheffer and Carpenter 2003).

Despite its ample use in ecology nowadays, the term threshold is used differently depending on the particular topic being addressed (see review in Groffman et al., 2006). Thus, thresholds might also be referred to as the points above which a particular property of the ecosystem under study has some value of interest (e.g., species reach above 50% rate of survival, Francesco Ficetola and Denoël, 2009). Although transitions towards this later type of thresholds might be linear, they might still affect other ecosystem features and make them exhibit transitions in a nonlinear way, especially if this threshold is mainly affecting the dynamical mechanisms of the system. For instance, changes in the sign of plant-plant interactions, from facilitative to competitive, may modify the dynamics of the ecosystem in drastic ways, thus affecting ecosystem features abruptly (e.g., spatial arrangements, Manor and Shnerb, 2008a), even if this change of sign occurs smoothly. In this thesis, I define thresholds as “characteristic values of biotic and/or abiotic factors driving shifts in the system that are either abrupt or that entail a major change in the dynamics of that system”.

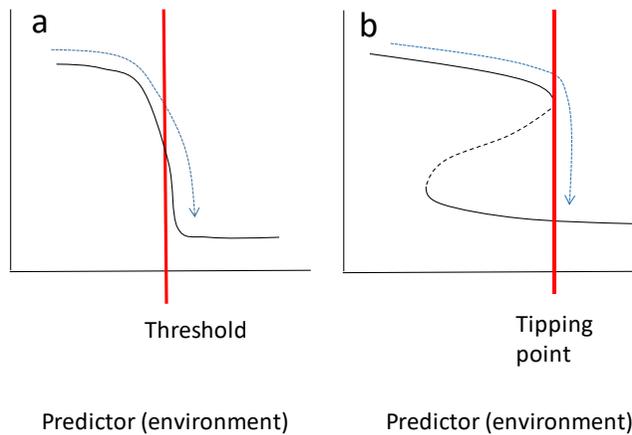


Figure 2.2. Threshold patterns.

Types of transitions in ecosystem state that might define a threshold value. a) Abrupt shift defining a threshold when a sharp decline of ecosystem state values begins; b) hysteretic shift between two alternative stable states (represented by full black lines; dashed lines represent unstable states) defining a threshold value in the tipping point (point in which a transition occurs from one stable state to the other). Blue dashed lines represent ecosystem changes with increasing values of the predictor. Red lines mark the threshold point.

Tracking ecosystem states and forecasting threshold behaviors as responses to external disturbances, such as climate change or the increase in livestock pressure, is important as it might entail abrupt and/or fundamental changes in ecosystem functioning (Verstraete et al. 2011, Mora and Lázaro 2013). For instance, the implications of catastrophic transitions from productive to desertified drylands, or from clean to eutrophic lakes, has generated an important body of knowledge in the development of early warning signals to prevent these transitions before they happen (Scheffer et al. 2009, Ditlevsen and Johnsen 2010, Kéfi et al. 2014). Early warning signals are changes in some ecosystem properties that might indicate the proximity of an abrupt transition. Such signals are basically of spatial and temporal nature. For example, ecosystems close to a catastrophic shift typically slow down their dynamical behavior against weak fluctuations (Scheffer et al. 2015). In other cases, ecosystems close to abrupt shifts may suffer important changes in the spatial distribution of vegetated patches. Spatial arrangement of vegetation in drylands may be characterized by regular (scale characteristic forms such as labyrinths, spots, stripes) and

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irregular (without a characteristic scale, so also known as scale-free) patterns depending on the interactions between species. Regular patterns arise when the system is dominated by competitive interactions, while irregular patterns are generated when facilitative interactions are prevalent (Scanlon et al. 2007, Manor and Shnerb 2008a, Kéfi et al. 2010b). Importantly, changes in environmental constraints (e.g., increases in water shortages or grazing) alter these patterns (Manor and Shnerb 2008a, von Hardenberg et al. 2010). Large plant patches in drylands tend to fragment with increasing aridity and may change patch size distributions in predictable ways, following a known sequence (for instance, in the case of regular patterns, from continuous cover to gaps, labyrinths and then spots before the collapse of vegetation, Von Hardenberg et al. 2001). Besides, there are clear dynamical consequences of the non-random spatial arrangement of the vegetation. For instance, in theoretical models, spatially arranged systems resist harsh conditions better than their spatially homogeneous counterparts (Von Hardenberg et al. 2001, Kéfi et al. 2010b, Getzin et al. 2016) and can also capture more resources and increase productivity (Puigdefábregas et al. 1999b, Boer and Puigdefábregas 2005a). As a consequence of their response to environmental changes and their influence on ecosystem dynamics and resilience, it has been hypothesized that spatial patterns of vegetation might change according to the proximity of a catastrophic shift to a more degraded ecosystem state, thus boosting up the interest of evaluating the role of the spatial arrangement of vegetation as early warning signals to detect such catastrophic shifts in advance (Rietkerk et al. 2004; Kéfi et al. 2007a, 2010, 2014)). Particularly, patch-size distributions (confronting patch sizes and the frequency in which they are observed) have been hypothesized to change from fitting a power law (when log-transformed frequency and patch sizes fit a straight line) to fitting a truncated power law (in which the slope of the line relating logarithm of the frequencies and logarithm of the patch-sizes exhibits a drastic change in the right part of the distribution) before critical transitions. However, there are still very few empirical studies aimed at assessing the validity of patch-size distributions as ecosystem monitoring tools. Some of them aimed at testing changes in patch-size distributions through degradation gradients at very local scales, and found evidences of changes in the patch size distributions (Lin et al. 2010, Moreno de las Heras et al. 2011). Other studies have not been able to link patch-size distributions to ecosystem functioning and casted

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doubts about the suitability of their use to indicate changes in ecosystem functioning (Kéfi et al. 2007a, Maestre and Escudero 2009, Bestelmeyer et al. 2013). Also, some studies called the attention about the fact that changes in patch-size distributions might not be easy to interpret as a dichotomical test on whether patch-size distributions fit power laws or truncated power laws (Pueyo 2011). This highlights the fact that we lack understanding on the types and mechanisms that drive the generation of patch-size distributions, which have not been successfully assessed mainly due to the lack of variability in the local studies performed to date.

Ongoing global warming will lead to increases in aridity in most regions of the world, which will both increase the environmental harshness experienced by dryland areas worldwide (Feng and Fu 2013, Fu and Feng 2014, Huang et al. 2015) and the global extent of drylands by 11%-23%, depending on the fossil fuel emission scenario considered (Huang et al. 2015). This increase in aridity will have strong effects on the composition, structure and functioning of drylands worldwide (see reviews by Maestre et al. 2012b, 2016), which are likely to happen in a non-linear way (D'Odorico et al. 2013). Therefore, it is of paramount importance to detect potential thresholds in the behavior of dryland ecosystems related to changes in aridity, which is a major component of ongoing climate change in drylands worldwide.

STATE OF THE ART: WHAT DO WE KNOW ABOUT THRESHOLDS IN DRYLANDS?

How do we study thresholds?

Although the study of thresholds in drylands is of paramount importance in the face of climate change and has been the basis of several research topics of interest (e.g., savanna transitions, shrub encroachment and desertification see, House et al. 2003, D'Odorico et al. 2012, Bestelmeyer et al. 2015), few empirical studies have claimed to identify thresholds (*sensu* Groffman et al. 2006) in drylands (but see Hoffmann et al. 2012, Mora and Lázaro 2013). In particular, very few empirical studies have identified alternative states in

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drylands (see Maestre et al. 2016), albeit they are specifically mentioned in some examples (Hirota et al. 2011). There are three main issues that prevent studies to elaborate on a well-defined basis about thresholds in drylands:

- i) Dryland studies are often limited by the range of conditions studied, and many empirical studies use linear regression methods to establish the relationships between variables of the system. Although nonlinear techniques are also applied in drylands (e.g., polynomial regressions, study of interactions and discontinuous regressions), few of them allow the identification of alternative stable states. Methods developed recently, such as the estimation of potential landscapes using observational datasets (Livina and Lenton 2007) allow tracking alternative stable states with observational data. However, the statistical power required for the identification of this type of patterns is very high, which prevents most studies to reach a proper identification and description of alternative stable states.
- ii) Threshold behaviors usually entail a profound transformation of the ecosystem, thus attaining many (if not all) components of the system at the same time. For instance, desertification involves a sharp decrease in ecosystem functioning, or large transformations of the ecosystem structure (Schlesinger et al. 1990, Reynolds et al. 2007). However, most studies on thresholds have only focused on a few components of the ecosystems (predominantly plant cover or spatial structure, see Manor and Shnerb 2008a; Kéfi et al. 2010; Bestelmeyer et al. 2013, but also soil erosion, see Chartier and Rostagno 2006; Mora and Lázaro 2013), ignoring other important components such as changes in ecosystem functioning or species composition (box 1).
- iii) Thresholds have been used with different meanings, as already pointed out in the previous section. The concept of threshold has been described with particular and discipline-specific terminologies within ecology, which hinders interdisciplinary exchanges of knowledge.

BOX. 1. Bibliographic analysis

We did a bibliographic analysis using the web of science (WoS) for dryland (“dryland OR arid*”), water limited (NOT “rive* OR estuar* OR ripar* OR wetland*”) ecosystems studying plants (“vegetation OR plant”) in which the effect of environment has been assessed (“(climate OR environment* OR abiotic OR temperature OR precipitation) AND gradient”) and thresholds has been identified (“shift OR threshold OR (alternative AND state) OR “resilien* OR catastrophic OR tipping”). We searched within these studies for those addressing spatial structure (“(spatial OR vegetation) AND pattern”), interaction web (“(species AND interacti*) OR facilitation OR competition OR (positive AND (feedback* OR interacti*))”) and composition and diversity (“(Community AND composition) OR diversity”) components of the ecosystem state. Also, we searched for those studies addressing ecosystem functioning (“function*”) and repeated all searches focusing on mathematical modelling studies (“model AND (math* OR dynamic*)”). We accommodated the number of studies of each type according to the framework proposed by (Tomimatsu et al. 2013); which considers three main ecosystem state components: diversity and composition, the interaction web and spatial structure; as well as direct and indirect (through ecosystem structure) effects of climate change on ecosystem functioning (Figure I).

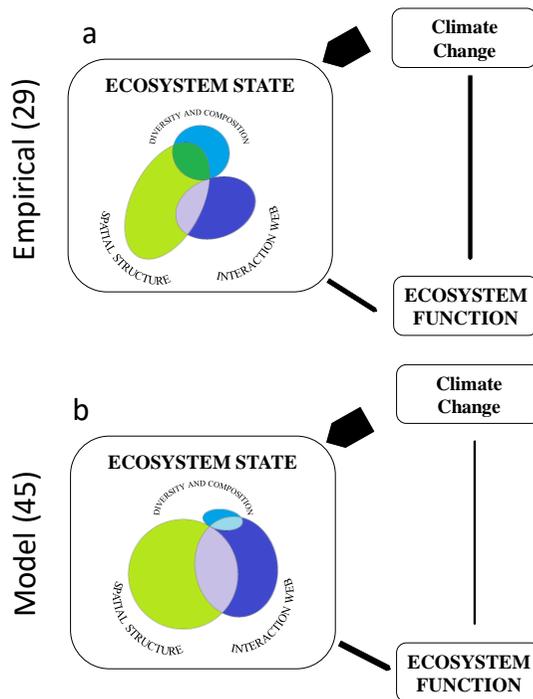


Figure I. Bibliographic search on Tomimatsu et al's (2013) framework for threshold studies. Results from a bibliographic analysis performed about dryland studies reporting threshold behaviors incorporated into Tomimatsu et al's (2013) framework. The search focuses specifically on resilience or catastrophic shifts studies that have used mathematical models (b) or empirical data (a). In the “Ecosystem State” box a Venn-Euler diagram is displayed representing three ellipses, one per each component of ecosystem state according to Tomimatsu et al (2013). The area of the circles is proportional to the number of studies involving each component of ecosystem states; overlapping areas are proportional to the percentage of studies including combinations of the different components. The size of the arrows between climate change, ecosystem state and ecosystem functioning is also proportional to the number of studies addressing links between each topic within the scope of the bibliographic search.

State of the art

Among the studies that claim to identify thresholds in drylands most of them identified continuous transitions towards certain values of variables, mostly morphophysiological at the species level (for instance, tree species would exhibit a clinal off-on response for use of water from upper soil layers, responding at particular threshold levels of summer precipitation input, e.g. Williams and Ehleringer 2000, or seedlings of some shrubs needing a minimum water availability to establish in deserts, e.g. León et al. 2011). However, there are a number of studies that are more focused on nonlinear responses of different aspects of the ecosystem state and functioning that suggest the existence of thresholds *sensu* Groffman et al. (2006).

Of particular relevance for managers and policy makers are those studies focusing on ecosystem functioning (in this thesis described as nutrient availability and cycling), which are hypothesized to undergo thresholds in processes such as desertification (Reynolds et al. 2007), but, are mostly studied indirectly through the examination of changes in plant cover patterns, mainly theoretically (box 1). Some empirical studies spotted environmental thresholds in drylands regarding soil erosion processes that might affect soil nutrient availability and plant composition and establishment rates (Mora and Lázaro 2013). Also a change in the processes involved in sediment removal from water to aeolian erosion at aridity thresholds around ~ 0.3 has been described (Ravi et al. 2007). Thresholds have also been found when studying soil formation at the edge of arid and hyperarid systems (Ewing et al. 2006) and nitrogen cycling at levels of Aridity Index ≈ 0.3 (Wang et al. 2014). Moreover, there are other studies that highlighted nonlinear trends in nutrient availability in drylands as a function of increasing aridity, which would suggest the existence of threshold patterns *sensu* Groffman et al. (2006). Among the later studies, the functional decoupling of nutrients is gaining momentum in drylands (Delgado-Baquerizo et al. 2013, Wang et al. 2014, Luo et al. 2016). The decoupling of nutrients occurs due to a nonlinear response of one of the nutrients when compared to the linear response of others, and it has been observed for nitrogen and phosphorous as a response

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to increasing aridity (Delgado-Baquerizo et al. 2013). These studies suggest important shifts in soil stoichiometry which may affect ecosystem structure and functioning in a nonlinear way. For instance, stoichiometric changes are hypothesized to select for species with different levels of nitrogen in their nucleotides, potentially altering ecosystem structural composition and functional traits (Peñuelas et al. 2012). Altogether, there are evidences that thresholds in soil nutrient availability might emerge as responses to increasing aridity in drylands. However, there is no threshold behavior (*sensu* Groffman *et al.*, 2006) described through aridity increases in soil fertility or nutrient cycling involving global gradients of aridity, which might importantly affect soil functionality with climate change. Additionally, there are a number of studies merging the functional composition of vegetation and ecosystem functioning (Lavorel and Garnier 2002, de Bello et al. 2010, Maestre et al. 2012a, Conti and Díaz 2013, Gross et al. 2013, Valencia et al. 2015). Among the results provided by these studies we find a clear link between the diversity of functional traits such as height and specific leaf area, which largely impact soil nutrient cycling (Lavorel and Garnier 2002, Violle et al. 2007), and ecosystem functioning (Conti and Díaz 2013, Valencia et al. 2015). Although these studies do not identify thresholds, changes in community composition might impact ecosystem functioning indirectly through trait compositional changes. In this regard, some studies show shifts in trait syndromes, such as changes from stress tolerant traits into stress avoidant traits through aridity gradients (Valencia et al. 2015) although the threshold nature of these shifts remains elusive.

Detection of thresholds in species composition or richness along environmental changes is, however, infrequent in community-level studies (Walther 2010). Some studies have identified compositional shifts throughout environmental gradients (Walther 2010, Mora and Lázaro 2013, Ulrich et al. 2014), but most of them are performed locally or regionally, and the threshold identified is not only climatic, but mixed with other disturbances such as encroachment or grazing (De Bello et al. 2006, Anderson 2007). An exception is the study by Ulrich *et al.* (2014), who analyzed patterns of beta-diversity in global drylands and found that profound compositional changes occur around 178 mm of rainfall (Aridity level calculated as 1-Aridity index ~ 0.88). Although it is likely that this pattern arises because species able to

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thrive in dryer habitats are specialized and drought-tolerant species, this remains to be elucidated. It is also unclear how this change in species composition may entail reorganization of ecosystem dynamics or functioning. Species extinctions also exhibit marked thresholds and cascading effects due to the interrelationships existing between the species involved (especially when trophic relationships are taken into account, see Allesina and Bodini 2004, Thébault et al. 2007, Rezende et al. 2007, Dunne and Williams 2009). Because some plant species in drylands may depend on the existence of others to survive (Bertness and Callaway 1994, Cavieres et al. 2006, Soliveres et al. 2015a), and because there are some species that are more influential than others for determining community structure through plant-plant interactions (Saiz and Alados 2011, Soliveres et al. 2014a), or ecosystem functioning (Sala et al. 1996, McLaren and Turkington 2010, Soliveres et al. 2016), thresholds in species extinction and ecosystem functioning might arise when the identity and the relationships between the species are jointly considered. Yet, very few studies have evaluated the vulnerability of plant ecosystems to cascading extinctions (Verdú and Valiente-Banuet 2008, Losapio and Schöb 2017) or to the loss of particular species or functional trait syndromes (Wardle and Zackrisson 2005, McLaren and Turkington 2010).

To understand how changes in species composition occur at the community scale, it is necessary to investigate how species assemble to form communities. As in many other ecosystems, community assembly of drylands is driven, among others, by abiotic filtering and plant-plant interactions (Weiher and Keddy 2001). Thus, studying the shifts in the relative importance of community assembly rules might inform us about the mechanisms involved in community compositional changes, especially those across aridity gradients, which is the main abiotic filter in dryland ecosystems (Kemp et al. 2003). The relative importance of biotic (competition and facilitation) and abiotic (mostly represented by environmental gradients) assembly drivers has been extensively studied (Keddy 1992, Cingolani et al. 2007, Kraft et al. 2015). However, there are still controversies involving the patterns they show through aridity gradients and their interactions with the species pool, especially regarding the capacity of plants to adapt to harsh conditions (Weiher and Keddy 2001, Chase 2003, Cingolani et al. 2007,

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Kraft et al. 2015). In particular, plant-plant interactions largely affect species composition, as they constitute a key filter during the assemblage of plant communities (Diamond 1975, Paterno et al. 2016). However, there is no consensus about the specific way in which plant-plant interactions modulate community assembly, and their importance through environmental gradients is still controversial (Grinnell 1917, Elton 1927, Lawton 1999, Ricklefs 2008, McCluney et al. 2012, Myers et al. 2013, Kunstler et al. 2016).

Understanding how positive plant interactions change along environmental gradients, and their role as drivers of diversity, has been a hot topic in community ecology for a long time (Callaway 2007, Brooker et al. 2008, Holmgren and Scheffer 2010, He and Bertness 2014, Soliveres and Maestre 2014). The interplay between facilitation and competition in drylands has been suggested to shift with increasing aridity although the shape of this relationship is still unclear (facilitation might wane with increasing harshness; see Holmgren and Scheffer 2010; Michalet et al., 2014; become more important under these conditions, see He et al. 2013; or being more related to species-specific features Liancourt et al. 2005; Soliveres et al. 2012, 2014a). Importantly, the studies that suggest a collapse in facilitation under extremely harsh environments (Tielbörger and Kadmon 2000, Maestre and Cortina 2004, Michalet et al. 2006) have not specified the environmental conditions at which this threshold may occur (see Soliveres and Maestre 2014).

Apart from the functional composition (through assembly rules of communities) and richness, plant-plant interactions have been hypothesized to affect other important ecosystem attributes such as the spatial pattern of plant patches (see Lefever and Lejeune 1997; Rietkerk and de Koppel 1997; Kéfi et al. 2007b; Scanlon et al. 2007; Manor and Shnerb 2008b). In particular, there has been many theoretical studies linking plant-plant interactions to different spatial patterns in drylands (Rietkerk et al. 2002, Kéfi et al. 2010b, Getzin et al. 2016), although there is still little empirical evidence to support these theoretical expectations (but see Xu et al. 2015). Indeed, there are very few empirical studies about spatial patterns, and most of them are performed over short ranges of environmental conditions (e.g., Kéfi et al. 2007a, Maestre and Escudero 2009, Lin et al. 2010, Moreno de las

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Heras et al. 2011). Such studies have already pointed out drivers other than plant-plant interactions that might be important for the formation of plant patches, including the existence of woody species (which can increase patch sizes, see Goslee et al., 2003, or promote patch merging via rhizomatous stems, see Lett and Knapp, 2003) or the relative importance of hydrological-aeolian sediment processes (Ravi et al. 2007, 2008). To tease apart these different mechanisms of patch formation, studies conducted across a variety of ecosystems, including different vegetation composition and environmental conditions are necessary. Importantly, there are clear links between the spatial arrangement of vegetation and ecosystem functioning (Aguiar and Sala 1999, Boer and Puigdefábregas 2005a), as it has been proposed that self-organizing plant spatial patterns increase ecosystem functioning (Puigdefábregas et al. 1999b, Mayor et al. 2013). While previous studies could not find a clear link between plant-plant interactions and ecosystem functioning (Mitchell et al. 2009, Maestre et al. 2010), the link between facilitation and ecosystem functioning mediated through the formation of spatial patterns remains to be explored.

CONCLUSION: IDENTIFYING GAPS

Our bibliographic analysis (box 1) indicates that most studies focusing on finding, describing and studying thresholds in dryland ecosystems have largely ignored the ecosystem functioning part of the framework proposed by Tomimatsu et al. (2013). Studying the emergence of thresholds in ecosystem functioning needs to be integrative, including the interplay between species interactions, spatial structure, species composition, changes in environmental conditions, and ecosystem functioning. Of particular importance in this regard is the inclusion of spatial patterns when studying thresholds in the response of ecosystem functionality to environmental changes, as they might act as early warning signals for the onset of catastrophic shifts (Kéfi et al. 2007a). It is also particularly important to consider the diversity and composition of plant communities, as they are key structural components that have been largely ignored in threshold studies (with the exception of the study of shrub encroachment, Van Auken 2000, D'Odorico et al. 2012). It

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has been consistently demonstrated that changes in plant composition affect ecosystem functioning in drylands (Flombaum and Sala 2008, Maestre et al. 2012a, Soliveres et al. 2014b), especially when this involves changes in the composition of functional traits (Allan et al. 2015, Valencia et al. 2015, Gross et al. 2017). Therefore, research on nonlinear responses of plant communities to environmental changes might be determinant in extending the study of resilience and environmental thresholds to ecosystem functionality. Theoretical studies on catastrophic transitions have rarely been, to my knowledge, carried out using community composition and diversity (but see Zavala and Zea 2004, Guerin et al. 2013, Ratajczak et al. 2016).

Plant-plant interactions have been identified as a key potential mechanism underlying the formation of plant spatial patterns in drylands (Scanlon et al. 2007, Manor and Shnerb 2008a, Kéfi et al. 2016). However, several issues obscure the understanding of how plant-plant interactions modulate spatial patterns and species composition, and how this relates to thresholds in ecosystem functioning. For instance, controversy about the importance of plant-plant interactions as assembly rules across environmental gradients (Tewksbury and Lloyd 2001, Brooker et al. 2008, Michalet et al. 2014) prevents us from evaluating whether this importance exhibits threshold-responses across environmental gradients that may easily scale up to larger shifts in ecosystem functioning (e.g., by producing changes in community composition or by altering the spatial patterns of vegetation). In particular, evaluating the importance of plant-plant interactions for community assembly as a function of environmental conditions and species-specific features is key because the uneven importance of species as drivers of community structure might cause cascading local extinctions if a few influential species are unable to cope with climate change (e.g., waning of facilitation because of the extinction of nurses; Verdú and Valiente-Banuet 2008, Valiente-Banuet et al. 2015).

OBJECTIVES AND CHAPTERS

In this thesis, I aim to investigate the existence of environmental thresholds driven by increases in aridity using a global dryland database gathered by an

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international research team led by Fernando Maestre (Maestre et al. 2012a, Ulrich et al. 2016). It is the purpose of this thesis to comprehensively study different components of ecosystem structure (spatial arrangement, community composition and plant-plant interactions) and functioning (multiple functions related to carbon, nitrogen and phosphorus cycling) to obtain a global view of ecosystem nonlinear changes with increasing aridity, and to identify and describe thresholds (sensu Groffman et al. 2006) if they are present. By doing so, I aim to provide a holistic framework on how and when dryland ecosystems may exhibit abrupt responses with increases in aridity, a major consequence of climate change in drylands worldwide (Huang et al. 2015) as well as understanding possible drivers of such thresholds. To do so, this thesis is organized in four chapters with the following specific objectives:

Chapter 1: Assess the types of spatial structure of vegetation found in drylands, as well as their drivers. This chapter focuses on the identification of types of patch size distributions and their drivers in dryland ecosystems worldwide. With this chapter, we aim to reveal some of the missing links between spatial structure and plant-plant interactions, and to build an empirical framework on the possible drivers of spatial arrangement in drylands.

Chapter 2: Evaluate the ability of patch size distributions of perennial vegetation in predicting thresholds in ecosystem multifunctionality (i.e. the simultaneous provision of multiple functions by ecosystems; Hector and Bagchi, 2007). This chapter studies the joint patterns of variations in multifunctionality and in two key vegetation features (i.e. spatial pattern and total cover) to: i) establish links between patch size distributions and multifunctionality, and ii) explicitly explore the presence of discontinuous shifts in multifunctionality across a global aridity gradient.

Chapter 3: Study the existence of environmental thresholds in the relative importance of community assembly drivers of global drylands. Using a novel approach to tease apart the influence of environmental filtering from plant-plant interactions in species' relative abundances, this chapter evaluates the

Introduction

relationship between the importance of plant-plant interactions and adaptive strategies of species across a large aridity gradient.

Chapter 4: Explore of the role of community compositional shifts on the emergence of bimodal patterns of multifunctionality in global drylands. In this chapter, we build upon the previous ones to investigate the role of species specialists on the emergence of bimodal multifunctionality patterns described in Chapter 2. We aim here to understand the link between multifunctionality, species composition and spatial pattern of the vegetation regarding the existence of threshold patterns.

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GENERAL MATERIAL AND METHODS

Study sites

This thesis is entirely based on a global field survey carried out in the context of the BIOCOM project, led by Fernando Maestre. As such, the thesis is conducted at regional/global scale.

We surveyed 236 dryland ecosystems across the globe (see Figure 2.1) using a standardized protocol that covered information from ecosystem structure (perennial vegetation cover, composition and relative abundance) and functioning (mainly soil fertility). We constrained our survey to arid (aridity index 0.05-0.2), semiarid (0.2-0.5) and dry-subhumid (0.5-0.65) ecosystems from all continents with dryland areas. This encompassed 19 countries all over the world (Argentina, Australia, Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, USA and Venezuela). The site selection captured a wide range in abiotic conditions (climate, elevation, soil type, slope), and biotic attributes (type of vegetation, total cover, species richness) of that existing in drylands. These areas did not restrict to pristine systems, but also included grazed, grass/fiber wood collection and hunting uses.

Mean annual precipitation and annual mean temperature of the study sites span the entire range found in dryland areas (excluding hyper arid areas, which usually have little or no perennial vegetation, Whitford 2002), and varied from 66 mm to 1219 mm, and from -1.8°C to 27.8°C, respectively. Most of the sites included in this study experience high seasonal variability in rainfall and seasonal drought, which varies in intensity and duration depending on location. The range of soil types present at the studied sites is also large, including more than 25 categories from the FAO classification (IUSS Working Group WRB 2015) and encompassing all main soil types present in drylands. Slope values ranged between 0.2° and 28°. To minimize the potential effects of different microclimates promoted by slope aspect, which can be very important in drylands (Kutiel and Lavee 1999, Gómez-Plaza et al. 2001), all sites that had slope values $> 2^\circ$ were located on SE-SW and NE-NW facing slopes in the Northern and the Southern hemispheres, respectively. Elevation varies between 69 m and 4668 m.a.s.l.. The sites

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surveyed encompass a wide variety of the representative vegetation communities found in drylands (grasslands, shrublands, savannas and open woodlands with shrubs). Perennial plant cover ranges between 3% and 83%.

Field data

Data collection took place between February 2006 and December 2012 using a standardized sampling protocol. In each site we established a 30 x 30 m plot representative of the vegetation of the zone. We displayed four 30 m long transects separated each by 8 m, starting from the upper left corner of the plot and orientated downslope. We used the line-intercept method to estimate the total cover in each transect, and averaged the four transects cover to obtain a plot estimation of total cover. We also placed 20 contiguous quadrats (1.5 x 1.5 m) along each transect and estimated visually the cover of each perennial vegetation species present within the quadrat.

We restricted our study to perennial plants because they are fundamental in maintaining ecosystem functioning and preventing desertification in drylands (Whitford 2002, Maestre and Escudero 2009). Moreover, annual plant composition in drylands shows a high degree of intra- and inter-annual variability (e.g. Pake and Venable 1996, Whitford 2002). Thus, we did not include these annual species to avoid confounding effects due to sampling “incomplete” communities depending on the time of the year and/or year sampled.

At each plot, we sampled soils in areas devoid of vegetation cover. We took five composite samples of 145 cm³ soil cores (0-7.5 cm depth), bulked and homogenized it in the field. We also took five soil samples below the dominant species of the plot. Soils were sieved (2 mm mesh), air-dried for one month and shipped to Spain to standardize the laboratory treatment of soil analyses.

Abiotic variables measurements

The main abiotic variable used in this thesis is the aridity level, which is obtained from Global potential evapotranspiration database (Zomer et al. 2008) by interpolating the GPS coordinates from our study sites. The global

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PET database uses WorldClim (Hijmans et al. 2005) interpolations to calculate the aridity index as annual precipitation divided by potential evapotranspiration (FAO). As this metric increases with milder conditions of aridity, we subtracted one to the aridity index obtained (which varies between 0.65 and 0 for drylands) to obtain a more intuitive measurement of aridity (Delgado-Baquerizo et al. 2013), which is called throughout the thesis Aridity level. Aridity is supposed to increase with climate change (Feng and Fu 2013, Huang et al. 2015), and is an important driver of functional (Maestre et al. 2012a, Delgado-Baquerizo et al. 2013, 2016, Valencia et al. 2015) and structural (Gross et al. 2013, Soliveres and Maestre 2014, Ulrich et al. 2014, Maestre et al. 2015, Le Bagousse-Pinguet et al. 2016) components of dryland ecosystems at regional or global scales.

SPECIFIC METHODOLOGY

We used a variety of methods in this thesis that are rather non-conventional in ecology and that derive from different fields. Although the methods are properly described in each chapter, here I want to briefly comment on some of the most unconventional. By doing this, I intend to introduce non-expert readers to the non-common terminology, to stress some particularities, and to present the background of the analyses used in this thesis.

Patch sizes extraction

In chapter 1, we used image classification to obtain vegetation patches of the zones of study. We did this because the transects of the field survey did not account for a sufficient number of patches to reliably estimate patch size distributions in most cases.

We used SAS planet (www.sasplanet.software.informer.com) to extract images from Google Earth and Virtual Maps of the sites surveyed in BIOCOM. The purpose of this analysis was to identify the vegetation and bare ground. As we did not require spectrometric measurements (we used the raw images obtained and RGB pictures sufficed to differentiate perennial cover) we did not performed any atmospheric correction of the images. There

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are different ways of image classification and the classification itself is a vast topic with complex terminology and requirements. Some image classification procedures are automatic, in the sense that a given rationale or threshold is used to differentiate the classes needed. We used supervised image classification, so we did several rounds of classification changing thresholds manually. To do this we used MATLAB image classification tools, which automatically selects color thresholds in the images. We supervised this classification and tuned the sensitivity of the classification parameters when necessary. Some features of satellite images might produce errors when performing classification. For instance, the season of the year in which the image was taken might produce some error caused by the bloom of annuals (which are avoided in the analyses and are not possible to differentiate in a satellite image). Therefore, we validated the classification using filed data of perennial cover.

Patch-size distributions and their fit to power law functions:

Patch size distributions relate the number of vegetated patches (interspersed in the bare soil matrix typical from drylands Tongway et al. 2001) and their sizes. This relationship usually follows what is called a power law (Newman 2005, Kéfi et al. 2007a, Scanlon et al. 2007). Studying power laws has some particularities and is a vast research topic in itself (Brown et al. 2002, Newman 2005). Power laws are scale invariant distributions which confer particular properties to the systems characterized by these distributions (e.g., maximize variance, shows fractal structuring, usually imply self-organization, see Gisiger 2001, Brown et al. 2002). In dryland ecosystems, it is hypothesized that power law distributions of patch size distributions may turn into truncated power laws when the system gets closer to desertification (Kéfi et al. 2007a, 2011); therefore, in this thesis we wanted to track variations in patch size distributions in the ecosystems studied.

Patch-size distributions are usually showed as inversed cumulative distributions (i.e., relating the patch size and the probability of finding a patch size larger than that in a log-log scale, see example in Figure 3.1). In such a graph, power laws look like a straight line. Truncated power laws show deviations from this straight line in the right part of the distribution.

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Also other distributions can appear related to patch size distributions, such as lognormal (Bowker and Maestre 2012) or exponential (Kéfi et al. 2011), which appear as curved lines in the inversed cumulative distribution. Fitting patch size distributions to power laws is also controversial, as these distributions are very sensitive to noise (White et al. 2008, Clauset et al. 2009). The most used approach to fit a power law to a distribution is the Clauset et al. (2009) methodology to find the two parameters defining the distribution (see further details in Chapter 1).

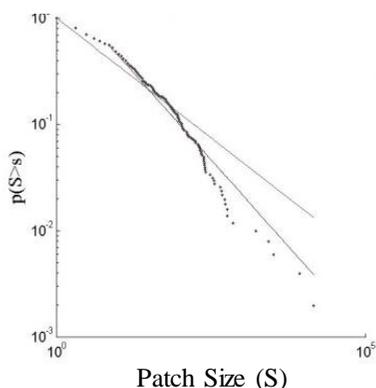


Figure 3.1. Example on patch size distribution.

Relationship between patch sizes and their frequency (probability of patch size being smaller than the patch size pool). This graph represents the inverse cumulative distribution of patch sizes with both axis log transformed. Line represents the fitted power law to the distribution.

Bootstrap and Monte Carlo approaches

Although bootstrap techniques are commonly used in ecology, it is worth to clarify here that this technique might be used to perform complex analyses using resampling techniques along gradients or with mathematical transformations.

Bootstrap is a method of re-sampling used to approximate the distribution of a statistic or metric (Manly 2006). Bootstrap techniques improve uncertainty estimations by allowing distributions of statistics to be non-normal. For instance, bootstrapping of a regression coefficient entail performing the same regression n times with different subsamples randomly picked from the original sample.

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Monte Carlo approaches feedback on bootstrapping methods but adding an intermediate step that usually entails mathematical transformations of the random subsamples taken (Manly 2006). Monte Carlo approaches are commonly used to generate random null envelopes of a mechanism or process, by assuming the mechanism to be tested as non-existing. The steps within any re-sampling processes are:

- Select randomly (or according to a rationale that always have a random factor) part of the samples.
- Perform analysis or calculations (if Monte Carlo, this entails mathematical transformations)
- Obtain output N times
- Summarize output (average, distribution or any other metric derived from N outputs file).

We used this approach several times in the thesis, especially to perform what are called moving windows. Moving windows do this sub-setting procedure along a gradient defined by a variable. Using moving windows allows depicting variations of some relevant metrics along a gradient which helps on gaining insights about the effect of the gradient on the metric studied. See more in the section non-parametric regressions, bellow.

Identification of thresholds

Identifying thresholds in ecology is challenging because most frequently used statistical techniques rely on linear assumptions (Francesco Ficetola and Denoël 2009). However, there are some techniques that permit the incorporation of non-linear behaviors. Perhaps the most used are polynomial regressions, or other logistic regressions, which fit datasets into known mathematical nonlinear constructs defined a priori. Also the inclusion of interactions in linear models introduce nonlinear functions into statistical fitting. Finally there are some few techniques that allow explicitly the search of thresholds in a relationship (see examples in Francesco Ficetola and Denoël 2009, Andersen et al. 2009, including regression trees or piecewise regressions), and other techniques that might be performed using bootstrap

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techniques to infer the existence of different stable states in the data (Livina and Lenton 2007). Here I summarize the ones used in this thesis:

Piecewise regressions

Piecewise regressions are discontinuous linear regressions that are commonly applied when a certain variable seems to change the slope depending on the range of values of the driver (Toms and Lesperance 2003). These regressions permit the identification of a threshold value that produces this change of slope. Mathematically, the equation to be fit to the data may be represented by:

$$y = b_1 * x + intcp_1 \quad \text{iff } x \geq x_{lim}$$

$$y = b_2 * x + intcp_2 \quad \text{iff } x < x_{lim}$$

Where x is the driver of y and b represents the slope of the regression and $intcp$ the intercept and x_{lim} represent the threshold value for x such that $b_1 \neq b_2$. There is a certain interdependence between x_{lim} , and both slopes and both intercepts, so that number of free parameters to be calculated in this regression is four (i.e., knowing x_{lim} and b_2 is not necessary to estimate $intcp_2$).

There are several methods to estimate piecewise regression, including the package segmented of R (Muggeo 2008), which subsets the data iteratively to find the value of x_{lim} that maximizes the difference between b_1 and b_2 (such as described by Crawley 2012).

Stability based tools: Potential landscapes

The dynamical behavior of any system might be represented by the so-called potential landscapes (Figure 3.2.a). They are continuous graphs based on the amount of energy/disturbance required to move the system out of a given state. Those represent the odds of change of the system using valleys (stable states, low potential) and hills (unstable states, high potential). Potential landscapes inform both about the most parsimonious converging state (stable

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state, by following the potential always towards lower values) and the dynamic rates of the system when is not at equilibrium (represented by the slope of the potential). Of course, the potential landscape changes with the conditions to which the system is imposed to (e.g., environmental conditions) (Figure 3.2.a). Therefore, the visualization of potential landscapes throughout parameter values representing these environmental conditions allows quantifying potential transitions of the system through a gradient of conditions (e.g., Figure 3.2.b). A common simplification of changes in potential landscapes across environmental gradients is to visualize the 3-D graph obtained with the potentials (e.g., Figure 3.2.b) from above and representing the conditions of the system in the x-axis and the fixed points of the state variables (bottom and top of the valleys) in the y-axis. Thus, for a given condition of the system we can identify the number, type and value of states, and depict their variation throughout different system conditions.

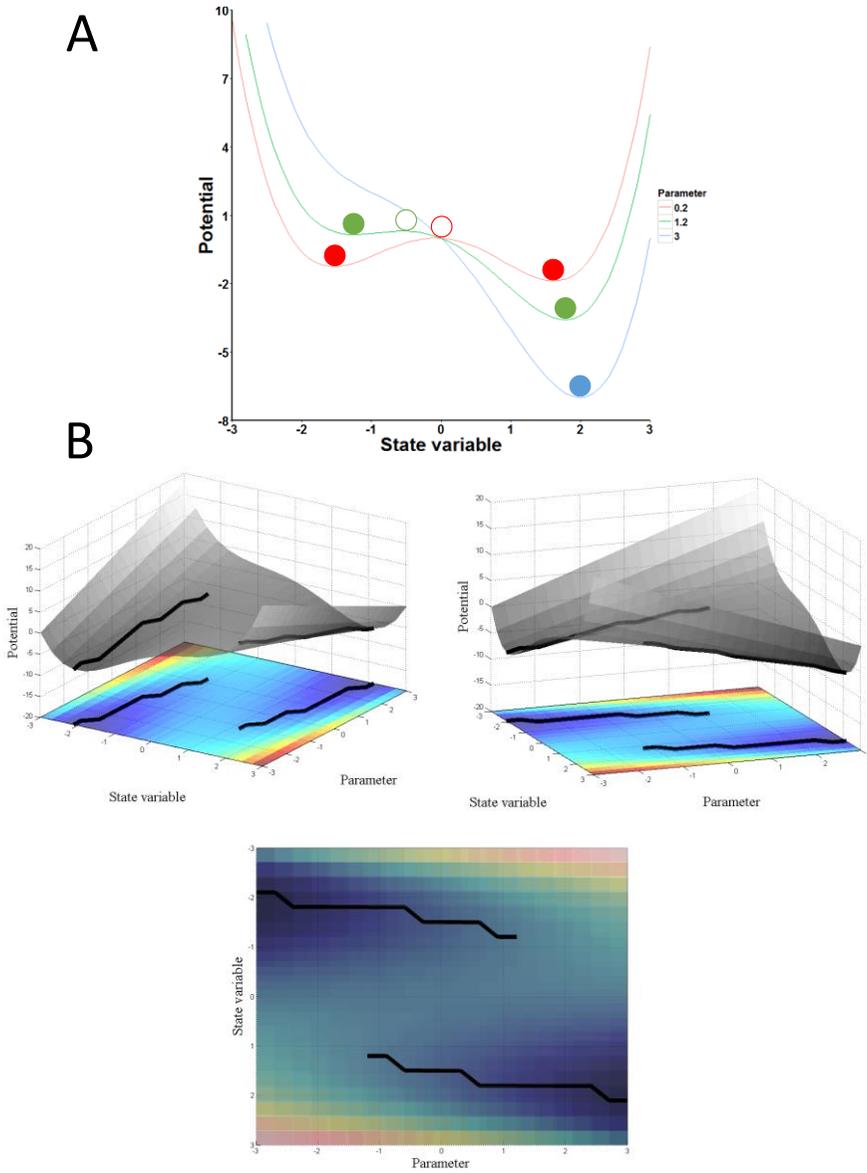


Figure 3.2. Stability potential and stability landscapes of a hysteretic system.

A) Potential landscapes for a system exhibiting two stable states for different values of a parameter. Filled balls represent stable states and empty balls represent unstable states. B) Different views of a 3D reconstruction of the potential landscapes exhibiting alternative stable states. Black lines represent stable states.

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Livina & Lenton (2007) developed a method to estimate potential landscapes from observational data. This method assumes that the value of any state variable will be found more frequently in an ecosystem snapshot if it is stable. This rationale entails that distributions of variables showing several modes might be exhibiting contrasting stable states, which is of paramount importance for the detection of thresholds, especially if these thresholds entail the existence of alternative stable states. This method needs large amounts of data to be reliable. Deriving from the notion that bimodal distributions might underlie contrasting states of the variable, we need to test whether apparently bimodal distributions are truly bimodal. To test this, analysis such as Gaussian Mixture Models might provide statistical tests for this. In this analysis, Bayesian and Akaike information criteria are used to differentiate the number of modes that best fit the distribution of the state variable.

Non parametric regressions: Moving window approach

Nonlinear behaviors are the basis underpinning the existence of thresholds. Of course some techniques such as quadratic or polynomial fitting might be used to assess nonlinear responses. Indeed, the most complex nonlinear regressions are gam or loess regressions, which coefficients are hardly summarized in a mathematical expression. However, there always are assumptions in the mathematical construct that is to be fitted to the data. Another way of implementing a nonlinear regression is using nonparametric regressions. Non parametric regressions are types of regression in which the relationship between the predictor and the response variable does not assume a predetermined form, but is built according to information derived from the data (Nadaraya 1964, Watson 1964, Kloeke and McKean 2014). Thus, these regressions need large amounts of data to ensure reliable results and are sensitive to overfitting. However they provide a unique tool for testing nonlinearities in the response of variables to external factors. There are several techniques of nonparametric regression, but almost all of them rely on the concept of moving windows (Altman 1992).

Moving windows are estimations on the response of one variable to another obtained by sub-setting the predictor and bootstrapping the response

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variable (by performing an analysis on the sub-set variable and showing the result, e.g., showing the distribution of a given functional trait value for a given range in aridity levels [e.g., 0.2-0.3] obtained by subsetting the entire range of aridity values sampled [e.g., 0.1-0.9]). The rationale underpinning moving windows is to obtain values of the response variable across subsets of the data that sequentially cover the whole range of the predictor value sampled. For complex statistical analyses such as Potential Landscapes or complex linear analyses, using moving window approaches allows depicting the trends of variation of a response variable throughout the driver without assuming any shape in their relationship. Also, when including interaction terms in linear analysis, using a moving window approach along the interactive term might be very useful to assess the type of interaction that is taking place (for instance, to depict whether the interaction transform a significant relationship in non-significant, or whether this interaction produces nonlinear variation along a gradient of the interactive term on the of one predictor upon the response variable). To perform a moving window analysis, the database is ordered according to the values of the predictor. A subset of N samples (being N sufficient as to perform the desired analysis) is then taken and the analysis is performed over these samples. The results are stored, the sample of the lowest value of the driver is discarded and the next higher value is added to the subset. Then the analysis is repeated and so on.

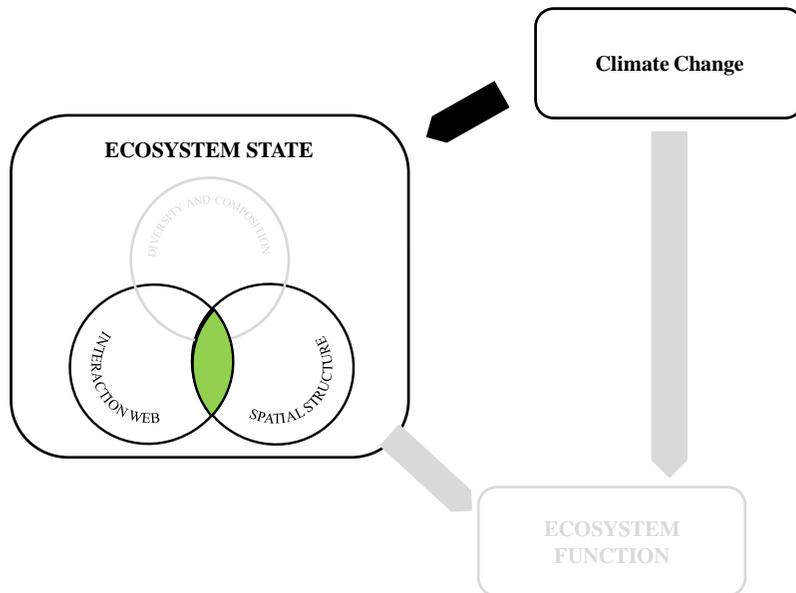
Species response to environment:

For Chapters 3 and 4, we assessed the niches of species gathered in the BIOCOM database. Species distribution models allow to reconstruct the species performance against abiotic factors (grinnellian realized niche, Grinnell 1917) using species distribution maps and abiotic variables maps (Guisan and Thuiller 2005, Elith and Leathwick 2009). Methods such as MAXENT (Elith et al. 2011) may be used to estimate the species response against a range of abiotic conditions, which is equivalent to the realized grinnellian niche of the species. In Chapter 3 of this thesis we used these models to infer the local adaptation to aridity of species in the places they were found in the field. SDMs basically perform nonlinear regressions between the occurrences of species in a global scale and the abiotic conditions of the places where they occur globally.

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CHAPTER 1

Spatial patterns of vegetation disentangle biotic and abiotic drivers in drylands



Miguel Berdugo, Sonia Kéfi, Santiago Soliveres, Fernando T. Maestre

Extended version of the first part of the manuscript: *Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands*. *Nature Ecology & Evolution*, 1, 0003 (2017).

ABSTRACT

The study of patch size distributions in drylands has increasingly gained attention as they may provide useful information as indicators of desertification. However, little is known about the factors driving changes in them, with only a few small-scale studies available to date. Here, we analyzed 115 dryland plant communities distributed worldwide to investigate their general typology, and to assess the relative importance of their potential drivers (plant cover, frequency of facilitation, functional traits of the dominant species, environmental factors). All the patch-size distributions analyzed were characterized by a heavy-tailed distribution with differing degrees of curvature, such as the power-law or log-series functions. We could consistently separate two types of patch size distributions based on their relative fitting to power law functions, one fitting mainly power law functions and the other fitting curved distributions such as a lognormal. These two types of patch-size distributions were driven by different factors; power law distributions were driven by facilitation and total cover, whereas those not fitting a power law were driven by aridity and the community weighted mean of height. These results suggest that contrasting dynamical mechanisms are responsible for the emergence of the two types of distributions (facilitation for PL-like and characteristics of individual plants and environmental harshness for the nonPL-like). We also show the important role that other largely neglected biotic attributes play as drivers of these distributions, such as relative woody cover.

Keywords: Spatial patterns, power laws, patch-size distributions, facilitation.

INTRODUCTION

Dryland (arid, semi-arid and dry-subhumid ecosystems; Middleton and Thomas 1992) vegetation is usually arranged in a two-phase mosaic formed by plant patches interspersed in a matrix of open areas devoid of perennial vascular vegetation (see Tongway et al., 2001, and references therein). The frequency of size classes of these plant patches can be characterized by heavy-tail distributions, which are related to changes in ecosystem functioning and, therefore, may provide information about the degradation level of drylands (Kéfi et al. 2007a, 2011, Manor and Shnerb 2008a, von Hardenberg et al. 2010). Mathematical models and field data suggest that patch-size distributions follow power law functions and that increasing environmental harshness (e.g. increasing droughts or grazing) causes a deficiency in large patches, thereby generating truncated power laws (Kéfi et al. 2007a, 2011, Manor and Shnerb 2008a, Lin et al. 2010). This has indeed been observed in field data (Kéfi et al. 2007a, Scanlon et al. 2007, Lin et al. 2010), but truncated power laws or lognormal functions have also been found to best fit patch size distributions in relatively well preserved ecosystems (Maestre and Escudero 2009, von Hardenberg et al. 2010). Besides, some studies stated that changes in patch-size distributions might not be easily classified dichotomically in power laws or truncated power laws (Pueyo 2011), thus highlighting the fact that we lack understanding on the types of patch-size distribution and mechanisms that drive their emergence empirically. Indeed, how different types of patch-size distributions differ across habitat-types of biogeographic regions is virtually unknown.

The sizes of plant patches are not only affected by environmental harshness, but also by biotic attributes such as plant-plant interactions (Kéfi et al. 2007b, 2016), functional traits of the dominant species (Aguilar and Sala 1999, Cortina and Maestre 2005, Maestre and Cortina 2005), plant cover (Maestre and Escudero 2009), and landscape features (Moreno de las Heras et al. 2011). These biotic factors likely interact with abiotic factors in complex ways to drive spatial vegetation patterns. They may thereby blur the potential of spatial patterns to predict degradation associated with increasing aridity or disturbance (Bautista et al. 2007, Maestre and Escudero 2009, Kéfi et al. 2010a, 2011). In particular, total cover is strongly linked to the formation of patch size distributions (Maestre and Escudero 2009). High cover communities tend to clump easily, forming characteristic large patch sizes which may alter the patch size distributions (Kéfi et

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al. 2011). Besides, plant cover has been proposed by other authors as better indicator of desertification processes than patch size distributions (Maestre and Escudero 2009, Bestelmeyer et al. 2013), hence it is of paramount importance to disentangle the interplay between patch sizes distribution and cover in order to know when patch-size distributions might be useful as alternative metrics of degradation processes.

Other biotic attributes characteristic of drylands, such as the encroachment of woody plants into former grasslands or the dominance of shrubs can also alter vegetation spatial patterns. Some authors have found that increasing shrub cover may entail increments in patch size (Goslee et al. 2003). Shrubs patches are subject to merge and can form dense patches via rhizomatous stems (Lett and Knapp 2003). Also woody encroachment may act through the composition of the patches (Maestre and Cortina 2005, Naito and Cairns 2011), which may change patch characteristics. Composition of the species in the patches may also affect the emergence of certain spatial patterns. For instance, community weighted plant height (CWH hereafter) describes the weighted size of the elements that will compose patches. Consequently, in a theoretical non-interactive community, this will be the main indicator for patch sizes (Xu et al. 2015a, 2015b). Patch size distributions of vegetation have been stated to follow primarily power laws, which are scale invariants (see Kéfi et al. 2011). Hence none of the parameters describing a patch size distribution (if following PLs) should be related to the size of its elements except in case power laws are dismantled and a predominant scale is emerging, which would be influenced directly by the averaged size of the plant individuals. Plant-plant interactions, which are the main driver of plant spatial pattern formation invoked (Rietkerk et al. 2002, Kéfi et al. 2007a, Manor and Shnerb 2008a, von Hardenberg et al. 2010, Meron 2015), also depend on the height of the species involved (Soliveres et al. 2014a). Facilitative interactions are supposed to merge patches of vegetation, thus creating clumps of patches with a bigger size, which underpin the formation of patch size distributions fitting to power laws (Kéfi et al. 2007a, Scanlon et al. 2007). Competitive mechanisms, on the other hand, tend to segregate plant patches, thus driving into lognormal-like patch size distributions, described better by the size of plants generating patches (Manor and Shnerb 2008a, Xu et al. 2015a).

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Overall, the current lack of understanding of the relative importance of biotic vs environmental drivers of vegetation patterns in drylands hinders our ability to use changes in patch size distributions as indicators of dryland degradation. In this study, we aim to investigate the vegetation spatial pattern in 115 drylands worldwide, spanning a wide range of environmental conditions, soil and vegetation types. We first overcome previous research limitations by performing a global-scale analysis of patch-size distributions. This allows us to assess the general typology of the shape of dryland patch size distributions. Second, we evaluate the relative importance of environmental (aridity) and biotic (plant cover, percentage of facilitative interactions and plant functional traits) factors as drivers of patch-size distributions. The latter will help to disentangle the obstacles due to the covariation between patch-size distributions and other ecosystem attributes regarding the potential role of patch-size distributions as reliable indicators of desertification.

MATERIAL AND METHODS

Study sites

We used a database of 224 30 m x 30 m sites in dryland plant communities worldwide (data from Maestre et al. 2012a), plus six additional dryland sites from Botswana that were surveyed in 2013 using the same methodology. Of these 230 sites, we retained those from which we could gather data on their patch-size distributions, community attributes and environmental conditions. The 115 sites retained are distributed over 13 countries (Argentina, Spain, Venezuela, Chile, USA, Iran, Morocco, Tunisia, Botswana, Kenya, Mexico, Ecuador, and Peru; see Figure 4.2.) and differ widely in their environmental conditions. Annual mean temperature and rainfall range from 2.6 to 25.7 °C and from 67 to 801 mm, respectively. The study sites also differ in their location, with elevations ranging from 76 to 4524 m.a.s.l., latitudes between -41° and 40°, and longitudes between -115° and 142°. Overall, the database includes 4 vegetation types (Grasslands, Shrublands, Open forest with shrubs and Savannah) which differ in species richness (2 to 39 perennial species) and total plant cover (see Maestre et al., 2012, for full details and dataset in Berdugo et al., 2016a).

Measurement of patch size distributions

For all field sites available, we downloaded VirtualEarth (<http://www.bing.com/maps>) and Google Earth (<https://earth.google.com>) high resolution satellite images (resolution $\leq 30\text{cm/pixel}$) using the software SAS.planet (<https://sasplanet.programas-gratis.net>). Although the use of satellite images and aerial photographs has limitations in environments with dense vegetation and when trying to estimate tri-dimensional spatial structures (Lefsky et al. 2002), the sparsely distributed plant cover at our study sites allowed us to use Google EarthTM and VirtualEarthTM to achieve the objectives of our study (see also Quets et al. 2013, Xu et al. 2015a). Both Google EarthTM and VirtualMapsTM data come from various sources such as satellite images and aerial photos, which present a range of different baseline spatial resolutions, varying from 0.1 m/pixel to 15 m/pixel (e.g., ~ 0.6 m/pixel of QuickBird imagery, ~ 0.4 m/pixel of GeoEye imagery, $\sim 0.4\text{-}0.5$ m/pixel of WorldView imagery, ~ 0.2 m/pixel of aerial photos, or ~ 0.3 m/pixel of DigitalGlobe imagery). In our study, we gathered only those images that provided a sufficient resolution to visually identify plant patches (resolution ≤ 0.3 m/pixel; with no clouds and homogeneous landscape around; see database in figshare: (Berdugo et al. 2016a) for the resolution of the images used at each site).

In most cases, the 30 m x 30 m sites surveyed in the field did not contain enough plant patches to obtain a reliable estimation of patch size distributions (White et al. 2008). To overcome this problem, we selected three 50 m x 50 m subplots close to each study site on the satellite images, such that one of them was placed exactly at the location of the original 30 m x 30 m site surveyed in the field. We used the Image processing toolbox in Matlab to perform image classification (MATLAB 2007), which allows image classification using the k-means method (Subbiah and Christopher 2012). This method partitions the pixels of the picture in clusters according to their luminance intensity (using a monochromatic version of the image). We used 30 clusters, ordering them from 1 (darkest pixels only) to 30 (the entire image). We classified the images by selecting the luminance threshold (from 1 to 30) able to detect all the vegetation pixels of the image by using the *graythresh* and *im2bw* functions from Matlab. The *graythresh* function uses Otsu's method for identifying a threshold in the luminance of a gray scale image that

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minimizes intra-class variance of the black and white pixels (Otsu 1979). We used this threshold as a first approximation for automatic classification of the image. In parallel, we visually classified the image using 30 different thresholds obtained by the k-mean classification analysis (Solomon and Breckon 2011). Then, we visually checked the images to ensure that the automatic classification was satisfactory when compared with that performed using expert knowledge. In 17.4% of the plots, the threshold selected by Otsu's methodology differed in more than 5 k-mean partitions from the one proposed by expert knowledge (which supposed deviations in estimated cover about 5-10%). In such cases we adjusted the luminance threshold to the one proposed by expert knowledge. Lastly, we validated the classifications by comparing the estimated cover of the images with the cover measured in the field. We related field measured cover with that extracted from the first subplot of the images (the one centered in the coordinates of the field survey), and only conserved those of which estimated cover was highly correlated with the one measured in the field (Pearson's $r \approx 0.7$ a threshold commonly used for assuming strong correlation between variables see Moore 2010). This reduced the total number of sites to 115 for further analyses. The cover estimated on the image of these sites correlated reasonably well with field measurements ($R^2 = 0.49$; slope = 0.66; intercept = 15.5) (See Figure S 4.1.).

Estimation of patch-size distribution parameters

For each site, we extracted all the patches and their sizes in each of the 50 x 50 m image plots after classification. We pooled all the patches for a given site and fitted a power law to their distributions. We used the approach of Clauset et al.(2009) to get the two main parameters of power law (hereafter PL) distributions according to the equation (Newman 2005):

$$p(x) = \frac{\alpha-1}{x_{\min}} \left(\frac{x}{x_{\min}} \right)^{-\alpha}$$

equation 4.1

where x represents the patch size and $p(x)$ describes the frequency of patches of a certain size. This equation represents the probability density function of a power decay. The parameters of the distribution are x_{\min} , the minimum patch size from which the fit to a power law starts (below that point data are discarded from the fitting procedure) and α , the rate of decay of frequency with patch sizes.

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When $p(x)$ and x are log-transformed, the inverse cumulative distribution, i.e., the frequency of patches larger than a certain size as a function of size, of a pure power law would appear as a straight line with negative slope (Figure S 4.2 and Figure 4.1). The approach used here calculates α using a maximum likelihood approach (Clauset et al. 2009) and estimates x_{\min} by comparing differences in the relative fitting of cumulative distribution functions (using Kolmogorov-Smirnoff statistic, KS, see Seiler and Seiler, 1989) of subsets of data with increasing x_{\min} . The KS statistic allows such comparison, which is possible even with samples of the same patch-size original distribution that differ in their N (caused by a different x_{\min} depending on the function adjusted). This statistic simply needs to be minimized for a given combination of x_{\min} and α , which happens in the combination that best minimizes both statistical fluctuations (estimated $x_{\min} > \text{real } x_{\min}$) and model deviations from proper fitting (estimated $x_{\min} < \text{real } x_{\min}$). This method allows the comparison of samples with different number of patches, provided that the function to be fitted is the same in the different subsamples. Also this approach allows fitting a power law function to all heavy tail distributions, including lognormal or truncated power laws, as even in these cases there is a fraction of the distributions that follows a power law. Sometimes the range of data remaining after discarding patch sizes lower than x_{\min} is not representative of the observed patch-size distribution, especially when the patch-size distribution is curved and best fits a lognormal function. To obtain an estimation of the range of patch sizes to which a power law could be fitted, i.e. the power law relative range (PLR), we used the following equation:

$$PLR = 1 - \frac{(\log_{10}[x_{\min}] - \log_{10}[x_{\text{smallest}}])}{(\log_{10}[x_{\max}] - \log_{10}[x_{\text{smallest}}])} \quad \text{equation 4.2}$$

where, x_{smallest} is the size of the smallest patch and x_{\max} the size of the largest patch in the image. PLR theoretically varies from 1 (all data fitted to a power law function) to 0 (no data fits a power law function). PLR is related to the shape of the distribution (understood as level of curvature, Figure S 4.3) and thereby to the goodness of fit to a power law (Figure 4.3.b), but is not exclusive to power law distributions (i.e. may be used for other heavy tailed distributions as well; e.g. simulated lognormal distributions fitted using this methodology had a PLR around 0.3-0.4). The use of the PLR allowed us to: i) compare all patch-size distributions among our sites, which vary from power law to lognormal, using a

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standard methodology for all of them (See Figure S 4.2), and ii) produce general descriptors of all the patch-size distributions evaluated, independent of whether they fitted better a power law or a lognormal function.

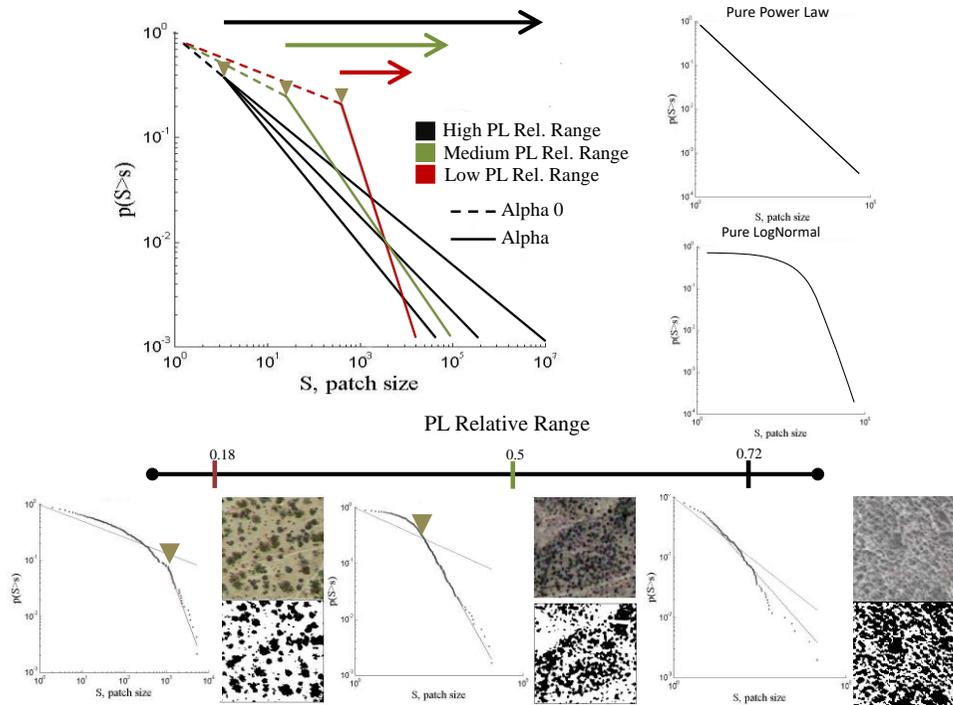


Figure 4.1. Meaning of power law relative range

Schematic representation of different patch-size distributions, confronting the logarithm of patch sizes (Log Patch Size) and the logarithm of their cumulative frequency (Log $P(S) < s$). Different colors show different ranges in patch sizes that follow a PL function: large (dark green), intermediate (red) and low ranges (light green). Dashed line (Alpha 0) indicate the decay of frequencies with patch sizes before x_{min} , patch size from which a PL initializes; represented as a grey triangle). Continuous lines (Alpha), instead, indicate the decay of frequencies with patch sizes after that point. Empirical examples with their metric values are shown.

Measurement of intrinsic and environmental factors

At each site, we measured three intrinsic community attributes known to influence patch size distributions: positive plant-plant interactions (facilitation, Kéfi et al. 2007a), plant functional traits of the dominant species (Goslee et al. 2003) and total cover (Maestre and Escudero 2009). Functional traits of the dominant species were measured in two ways: i) the relative dominance of woody plants in the

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community, measured as the fraction of total cover occupied by them (relative woody cover; RWC hereafter) and ii) the community-weighted average plant height, where data was obtained for those species accounting for 80% of the total cover (CWH hereafter; data from TRY; Kattge et al., 2011). As a measure of positive plant-plant interactions at the community-level we used the percentage of facilitated species. This index measures the proportion of species more associated with a given nurse than expected by chance. It compares the number of individuals found in open bare sites vs. those found under nurse species, calculating a χ^2 metric of each pairwise interaction (see Soliveres and Maestre, 2014 for full details). Facilitation was measured in a subset of 71 sites. Lastly, the total plant cover was estimated using the line-intercept method along four 30-m long transects within each site, plant cover ranged from 4% to 83% in our study sites.

Climatic data were obtained from Worldclim (Hijmans et al. 2005) to calculate the aridity level within each site, measured as $1 - AI$ (where AI [Aridity Index] is precipitation/potential evapotranspiration). Thus, high values of the aridity level correspond to high levels of drought stress (Delgado-Baquerizo et al. 2013). The aridity level ranged from 0.94 to 0.53 in our 115 study sites, encompassing semiarid and arid drylands.

Statistical analyses

Describing the general topology of patch-size distributions

While patch-size distributions with a high PLR clearly fit to a power law function, it is unclear to which distribution is fitted those with low PLR (Clauaset et al. 2009, Pueyo 2011). In order to overcome this limitation we performed regressions between the parameters describing the patch-size distributions to find patterns of variation that could describe the general shape of patch size distributions found in our study. All variables selected describe geometrical properties of the curve representing cumulative patch-size distributions as it was divided in two zones: the first decay up to x_{\min} and the second one, which fits power laws up to x_{\max} . We performed simple regressions using the different parameters of the patch size distribution as response variable of PLR. These parameters were:

α_0 : corresponding to the exponent of decay of frequencies with patch sizes of a theoretical power law that stands from the minimum patch size

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observed in the distribution to the x_{\min} value obtained by Clauset et al. (2009). This parameter respond to the first part of the decay of frequencies with patch sizes (which is discarded by Clauset methodology and that does not necessarily have to follow a PL). The interest of this parameter stands on the relationship with PLR. If the slope of this relationship is high, it means that the higher x_{\min} values are matched with a strong decay in frequencies of patch sizes. This will not happen if the power law deviates to other distribution such as lognormal, in which the frequency of different x_{\min} should be maintained with high x_{\min} values and, hence, the relationship α_0 -PLR should have smooth slopes.

α : corresponding to the exponent of decay of frequencies with patch sizes of the distribution part that follows a power law (i.e., the right part of the distribution when divided by x_{\min}). In theory, the value of α should remain independent on PLR if the function that best describes patch size distribution is a power law. If alpha is not independent of PLR, the later is marking a geometric property of the patch size distribution that condition slope values in the last part of the distribution. This is not expected unless external causes are shaping the distribution (for instance, smaller patches do not follow a power law because the emergence of a curve) and, hence, the patch size distribution fits better to heavy-tailed functions other than power law.

x_{\max} and x_{\min} : corresponding to the maximum and minimum patch sizes and the initialization point of a power law. These parameters are involved in the calculation of PLR. Hence, according to eqn 2, we expect PLR to decrease with higher x_{\min} or lower x_{\max} . This relationships indicate how is the PLR shortening. For example, if we find that there is no relationship PLR- x_{\min} but there is a positive relationship PLR vs x_{\max} , that means that less PL-like distributions are associated with a decrease in the size of larger patches. If PLR vs x_{\max} showed no significance but there is a negative x_{\min} PLR relationship the PL-like behaviour is mainly a consequence of the shape of the distribution (it is shortening from the left side of the distribution). If both relationships are significant, this will mean that low PLR values correspond to both higher x_{\min} and lower x_{\max} , indicating that both the shape

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of the distribution and the maximum size of the patches are acting in tandem for shortening PLR.

a parameter: corresponding to the quadratic term of a polynomial fitting to the inverse cumulative function of patch-size distribution. This term indicates the shape in a second degree polynomial. The resulting line from the fitting is concave if $a > 0$, convex if $a < 0$ and straight line without curvature if $a = 0$.

Identifying types of patch-size distributions

Although the PLR provided us with a general continuous descriptor of patch size distributions, we wanted to evaluate if there were general types of distributions in our data. Different types of distributions might be reflecting contrasting drivers in vegetation spatial self-organization and, thus, it is worth to explore their functional implications (Kéfi et al. 2007a, Scanlon et al. 2007, Manor and Shnerb 2008a, Bowker and Maestre 2012). We did so using two complementary approaches.

First, we performed a correlation between PLR and the log likelihood fitting indicator between pure power law and lognormal distribution. We selected these two distributions because they represent opposite mechanisms in patch size distributions (competition driven, such as shown in Bowker and Maestre, 2012 versus facilitation driven such as shown in Kéfi et al., 2007a, Scanlon et al., 2007). For doing this analysis, we extracted the log-likelihood value of a pure power law that stands over all orders of magnitude of each distribution. Then we subtracted to this value the log-likelihood resultant from fitting the same data to a lognormal distribution. This analysis should be taken carefully. In order to compare both log-likelihood values, they must be extracted from the same set of data (i.e., having the same N). Clauset's methodology extracts power law parameters and log-likelihood metrics, but it sequentially changes x_{\min} value to do so. As a consequence, patch sizes lower than x_{\min} value, are discarded and are not taken into account for the calculation of the log-likelihood value. Hence, a pure power law must be fitted, instead of one taken from Clauset's fitting (Clauset et al. 2009), which would influence the number of data that are fitted in this distribution. According to the subtraction ($PL - \text{Log}N$) and given that a higher Log likelihood value indicates a

better fit, the higher the Log likelihood value, the best fit to a power law rather than to a lognormal function.

It is not clear to what would power law distributions turn into along under the influence of external disturbances (Kéfi et al. 2007a, Pueyo 2011, Bowker et al. 2013). Additionally, it is not possible to compare distributions with different numbers of samples (which happens because of the existence of x_{\min} , although we can compare pure power laws as in Figure 4.3. if we assume that this parameter does not exist). Thus, we searched for changes in the properties of the topology of patch size distributions that could indicate a drastic change in vegetation spatial organization. Changes in the pattern of variation of geometric characteristics of distributions (describing their shape) might be related to changes in the distribution that the patch-size distribution is following. This analysis is aimed at finding geometric shifts in patch-size distributions, thus avoiding the problem of defining a particular distribution to be fitted and compared with power laws. In particular, the parameter α represents a key property of power law functions related with its scale-invariance. Thus, we searched for discontinuities in the relationship between PLR and α , as a signal of scale-invariance disassembly. As mentioned above, the α value of power laws is supposed to remain constant regardless of the idiosyncratic difference between sites, most likely because the emergence of power laws is favored by plant-plant facilitation mechanisms that underlie the processes of vegetation pattern formation in drylands (Rietkerk et al. 2002, Scanlon et al. 2007, Manor and Shnerb 2008a). This rationale is presented in (Clauset et al. 2009). Variations in PLR (produced by changes in x_{\min}) will produce variations in α values only if the distribution is not scale-invariant and, therefore, does not fit to a power law. To split the data set in two subsets according to the relationship found between PLR and α , we performed linear regressions to subsets of the data by sequentially discarding the sites with lower PLR. When the relationship between PLR and α became non-significant ($P > 0.05$), we interpreted it as the separation between these two subsets of data. Additionally, we performed piecewise regressions between PLR and α (see Appendix 1.1).

Identifying the drivers of the types of patch size distributions observed

Modifications in the type of patch-size distribution might be linked to changes in the ecological processes driving them (Rietkerk et al. 2002, 2004). To test this, we

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evaluated the responses of patch-size distributions to changes in total plant cover and aridity using structural equation models (SEM, Grace 2006). After identifying the main parameters describing patch-size distributions in the analyses explained above, we performed SEMs to assess the relative importance of biotic and abiotic attributes of our sites as drivers of these parameters. SEMs assess multivariate causal relationships by comparing the (co)variance structure of the data with an a priori model that identifies plausible causal relationships among the variables introduced based upon previous knowledge. SEMs test whether the data are satisfactorily fitted to this model, assigning a standardized weight, or coefficient, to each causal relationship or path (Grace 2006). The path coefficient is directly analogous to a partial correlation coefficient and is interpreted as the size of an effect that one variable exerts upon another. The statistical significance of each path coefficient (whether or not it is equal to 0) was tested using bootstrapping methodology, which is robust to departures from normality in the data. We built a model accounting for direct and indirect effects of aridity and biotic variables (total cover, CWH and RWC) on the attributes of patch-size distributions. We chose biotic variables that may correlate with patch characteristics such as CWH (Aguilar and Sala 1999, Maestre and Cortina 2005) and RWC (Goslee et al. 2003, Lett and Knapp 2003) and total cover as its relationship with patch-size distributions is subject of discussion (Maestre and Escudero 2009, Kéfi et al. 2010a, Bestelmeyer et al. 2013). Since we found the relationship between the different parameters of patch-size distributions to be strong (Figure 4.2.), we introduced a link between these variables. For SEM analysis five sites were removed due to lack of data on CWH. For the plots in which we had facilitation measurements (71), we also used the SEM approach adding facilitation as another predictor.

SEMs were performed using AMOS (Arbuckle 2014). Regressions were performed using R (R Development Core Team 2008). Dataset and codes used are available from figshare (Berdugo et al. 2016a, 2016b).

RESULTS

The typology of patch size distributions

Image analyses showed that the patch-size distributions of all 115 sites were heavy-tailed with varying levels of curvature (Figure S 4.2). In curved distributions, only a range of the patch sizes fits a power law. This range is referred to as “Power Law Range”, PLR, and is used as a proxy of how well the distribution considered fits a power law (Figure 4.3. b). Two parameters were extracted from the fits: α , which represents how fast the frequency of patches decays with their size and the PL relative range, i.e. the range of values over which the data fitted to a power law. Neither alpha nor PLR varied with latitude and longitude (see Figure 4.2.).

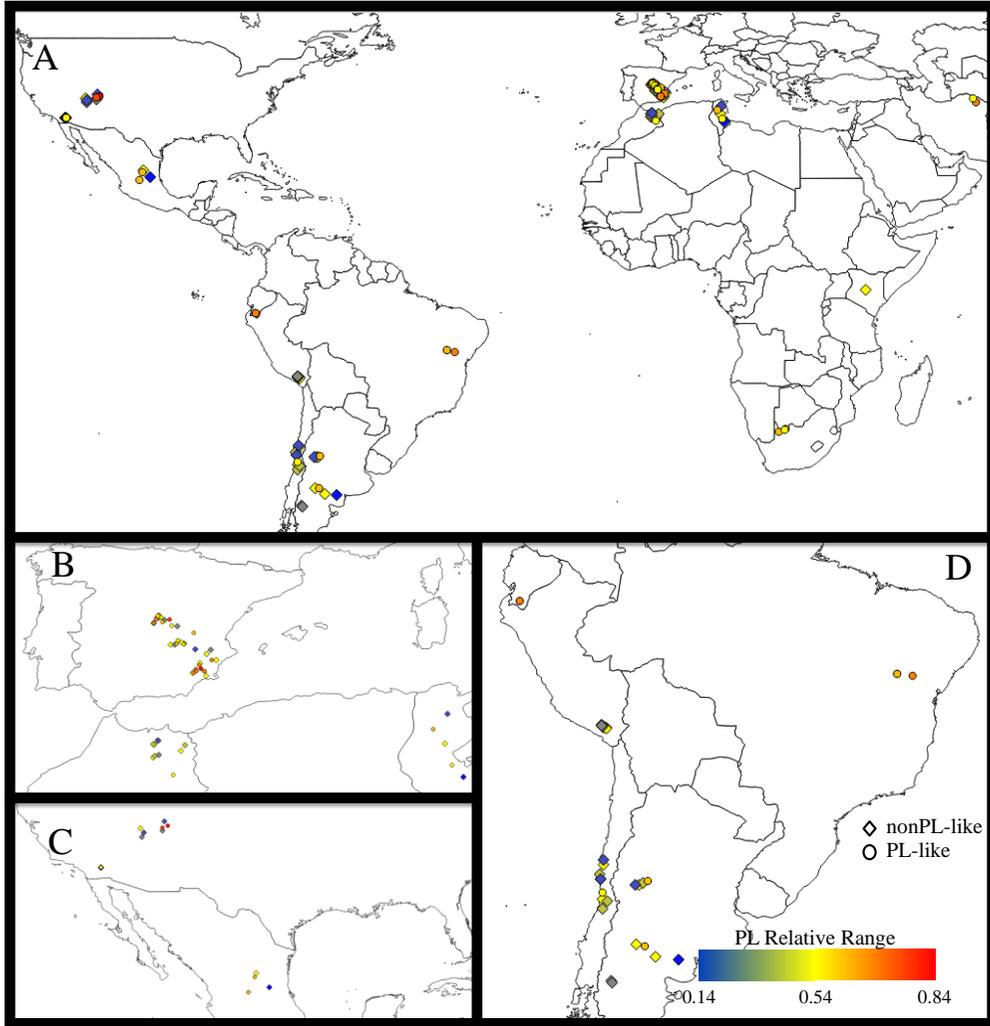


Figure 4.2. Map of patch-size distributions

Map of the sites analysed during the study. Circles indicate nonPL-like sites; diamonds indicate PL-like sites. The colour switch from blue to red according to the value of PLR. A: Map of the world; B: Zoom on Mediterranean area; C: Zoom on North America area; D: Zoom on South America area

For a number of sites in our data set, the estimated α of the patch size distributions was found to be very similar across sites (Figure 4.3. a). However, in a subset of sites characterized by low PLR values, we found a strong relationship between PLR and α (Figure 4.3.a). Moreover, in those sites, PLR was the strongest driver of α (see Figure 4.4.), meaning that the slope (α) was (almost exclusively) a consequence of how much the distribution deviates from a pure power law. These

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results suggest that two ranges of PLR are defining two types of distributions. The threshold identified by this methodology was very similar to that found when comparing the relative fitting of pure power laws (without x_{\min} , i.e., fitted to all the patches of the data) versus lognormal distributions (Figure 4.3.b). Other methods to subset our data into two types of patch-size distributions, based on piecewise regressions of PLR versus α also yielded thresholds consistent with the one described here (Appendix 1.1). The first type (found in 63 out of the 115 sites) was characterized by PLR lower than ~ 0.57 and negatively related to α (see Figure 4.3.). These sites were generally best fitted by lognormal functions (Figure 3.3.b). The sites were characterized by a low plant cover (Figure S 4.4a), high aridity values (Figure S 4.4b), smooth decays in frequency from smallest patch size to x_{\min} (Figure S 4.3a), low values in the maximum patch size (Figure S 4.3d, Figure 3.1) and curved-like distributions (Figure S 4.3e). The second type of patch-size distributions (found in 52 sites) was characterized by large PL relative ranges (> 0.57) which were not related to α , and they were best fitted by pure power law functions. We refer to these two groups as ‘non PL -like’ and ‘PL-like’ sites, respectively.

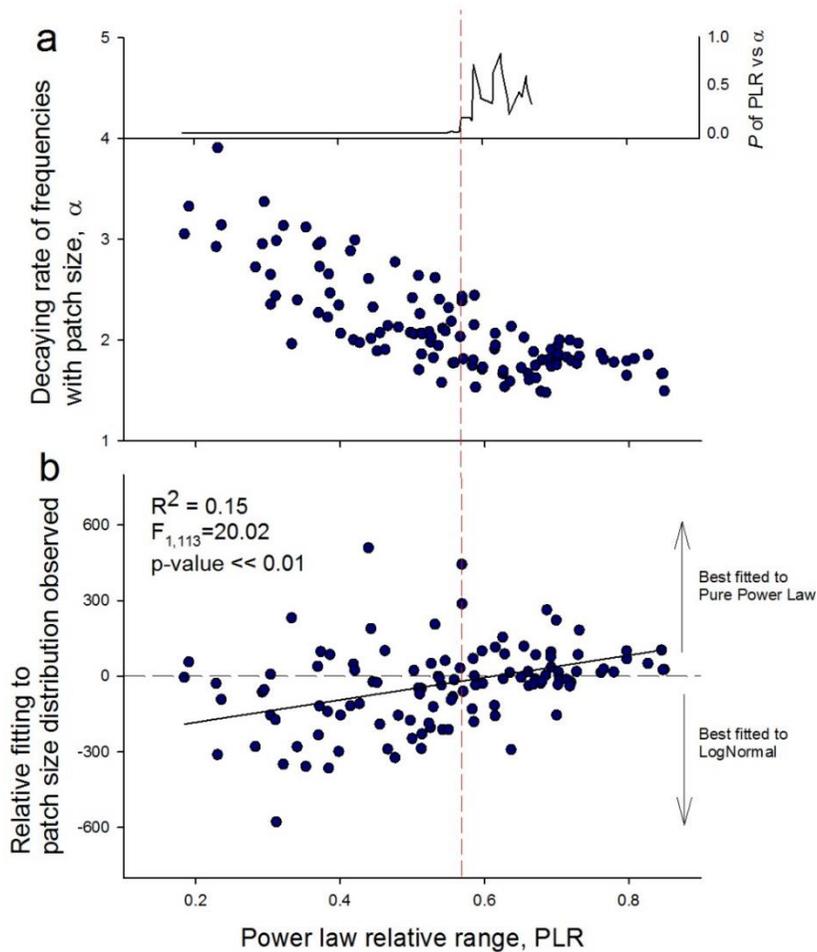


Figure 4.3. Types of patch size distribution found in global drylands.

a) Relationship between α (slope of the distribution) and the power law range (PLR, the fraction of the distribution that follows a power law) in the 115 sites studied. Upper panel: P value of the relationship (i.e. linear regression) between PLR and α obtained by iteratively discarding sites with lower PLR. The discontinuity point in the relationship between PLR and α is indicated by the dashed red line (i.e. point such that $P > 0.05$). b) Relative fit of patch size distributions to a power law versus a lognormal as a function of PLR measured as the differences of the log likelihood of a pure power law distribution (fitted on all patch sizes) and a lognormal distribution. The line represents the linear regression fitted, whose statistics are shown. Dashed black line indicates no difference between the fit to a power law or lognormal function.

The relative importance of biotic and abiotic drivers

When analyzing non-PL and PL-like sites separately using SEMs, we found changes in the relative importance of the different predictors of their attributes (PLR and α). In PL-like sites, biotic attributes (total cover and plant height) were more important than aridity in determining PLR and α . Aridity only had an indirect effect on the PL parameters via total plant cover (Figure 4.4a). Conversely, in the non-PL sites, we found a direct negative effect of aridity on PLR, as well as a decoupling between plant cover and aridity and between cover and PLR. Contrary to the PL-like subset, plant cover was the least important driver of α , which was driven mainly by other biotic attributes (plant height and the percentage of woody cover) and was strongly, positively, related to PLR (Figure 4.4b). None of these results was driven by a different range on data values (see similar ranges of both total cover and Aridity in Figure S 4.4. for both patch-size distribution typologies).

In the subset of sites where facilitation was measured, the percentage of facilitated species was positively related to PLR for the PL-like sites (Figure 4.4.c) but not for the nonPL-like sites (Figure 4.4.d).

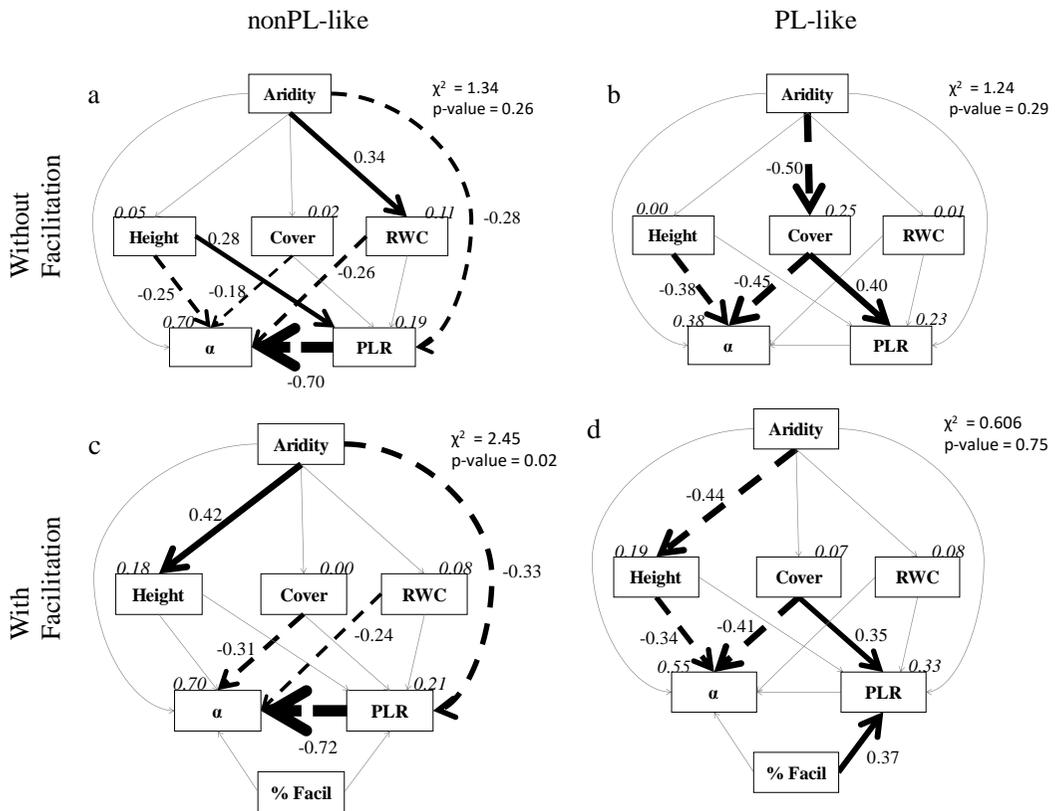


Figure 4.4. Drivers of patch size distributions.

Structural Equation Models (SEMs) for PL-like (B and D) and nonPL-like (A and C) sites. SEMs including facilitation as predictor for those sites in which this measure was available are shown (D, N = 31 and C, N = 40). Grey and black lines indicate non-significant and significant paths, respectively. Full or dashed lines indicate positive or negative relationships, respectively. The standardized patch coefficient of each significant path is given. The amount of variance explained (R^2) for each endogenous variable (those with arrows pointing to them) and overall goodness-of-fit (χ^2) of each model are given. TCT: Total cover; RWC: Relative Woody Cover; Alpha: exponent of decay of frequencies with patch size for the data that could be fitted to a power law distributions; PLR: percentage of orders of magnitude that follow a power law; Height: community weighted plant height (in cm).

DISCUSSION

Typology of patch-size distributions:

It has been previously documented that patch size distributions fit a power law function (mostly straight line between the logarithm of patch sizes and that of their frequencies Scanlon et al. 2007, Lin et al. 2010, Moreno de las Heras et al. 2011) and that they depart from these distributions towards truncated power laws when the system is disturbed (Kéfi et al. 2007a, Lin et al. 2010). Our global dataset confirmed these previous results and extended them to a wide variety of dryland communities. Our results confirm the general spread of heavy tail distributions in dryland patch-size distributions, although it might be noticed that these general results might not hold for communities with regular spatial patterns as they have a dominant patch size (Deblauwe et al. 2008). The truncation of power law patch size distributions has been associated to reductions in the frequency of large patches in comparison to a pure power law (Kéfi et al. 2007b, 2011, Lin et al. 2010). However, we also observed patch-size distributions to deviate from power law functions by losing not only of the large but also of the small patches (as shown by the curvature not only on the left but also on the right part of the patch-size distribution; Figure S 4.3). Although not expected in theory, this type of truncation has been shown in empirical studies (Bowker et al. 2013, Quets et al. 2013) and in theoretical studies simulating low colonization rates of vegetation (Marani et al. 2006) or high run-off conditions (von Hardenberg et al. 2010). The loss of small patches with increasing environmental harshness could be explained by reductions in the number of recruited seedlings under harsh environments (Weltzin and McPherson 1999), or with reports of a low number of isolated individuals in ecosystems dominated by facilitation (Bertness and Callaway 1994, Soliveres et al. 2014a).

Interestingly, a detailed analysis indicated that there is a discontinuity in the relationship between PLR and the α parameter of a PL (i.e. its slope). This result emerges from the relationship between PLR and the maximum patch size of the distributions (see Figure S 4.3.d) and produces a sudden shift in the relationship between PLR and α when large patches start to collapse. Power law distributions, however, should be scale invariant, which means that the decay of frequencies with

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patch sizes (α) should be consistent regardless of the range of patch sizes that fit a power law function (Clauset et al. 2009). Moreover, because the scale invariance is due to the mechanisms forming the power law (facilitation, see Scanlon et al. 2007), it should be robust to idiosyncratic differences between study sites (such as the size of the plants, the number of patches or even the total cover of the site). Therefore, the strong relationship between scale derived metrics (PLR) and α found in our sites is unexpected, and it is likely a consequence of a change in the processes driving the formation of vegetation spatial patterns. This relationship was driven by a subset of the studied sites with low PLR (Fig. 1), and these low PLR values might indicate a lack of scale invariance of such distributions. Since this scale invariance (suggested by α values) can only change if the processes forming the spatial distribution are different, we interpreted the discontinuity in the relationship between PLR and α as an indicator of two types of patch size distributions, which differ in the processes driving plant spatial patterns. As a result, we separate distributions in two types: i) in which PLR strongly controls α and produces curved-like distributions characteristic of sites with high aridity and low cover (nonPL-like); ii) in which there is not relationship between α and PLR which fit power laws on larger ranges and are characterized by high cover and low aridity values, (PL-like). Thus, sites with low PLR values (nonPL-like subset) reflect the loss of large patches, as predicted for degraded or stressed environments (Kéfi et al. 2007a, 2011, Lin et al. 2010, Moreno de las Heras et al. 2011).

Factors driving the shape of patch-size distribution:

Spatial patterns of dryland plant communities are not always related to total cover (Bautista et al. 2007, Kéfi et al. 2011, Zurlini et al. 2014) and therefore the study and monitoring of both variables together is recommended (Li and Reynolds 1994, Proulx and Fahrig 2010). Indeed, whether or not these attributes depend on each other has raised substantial debate regarding which of them should be used to monitor the onset of desertification (Maestre and Escudero 2009, Kéfi et al. 2010a, Moreno de las Heras et al. 2011). This is the first study showing a consistent disconnection between patch-size distributions and total cover over a wide range of conditions worldwide. The immediate implication of this finding is that patch-size distributions are informing about the state of the system in a way that is not reflected in the total cover, revealing the importance of patch-size distributions as complementary indicators to total cover. We also found a clear link between aridity

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and total cover in PL-like sites that was not found in nonPL-like sites (Figure 4.4.b). Water availability is the major limiting factor for plant growth in drylands, and therefore the tight link between aridity and cover in non-degraded systems is expected. However, in fragile/degraded systems, plant cover may depend more on disturbance (e.g., overgrazing) than on climatic factors (Kéfi et al. 2007a, Lin et al. 2010), which may explain the low explanatory power of aridity on plant cover in these sites.

It has been suggested that interactions among species are main drivers of spatial pattern formation through a process of self-organization (i.e., a process by which parts of the system interact locally generating emerging properties at larger scales; Solé & Bascompte 2006; Rietkerk & de Koppel 2008). Our field data confirm the importance of plant-plant interactions in the PL-like sites but not in the nonPL-like ones. In the latter sites, the distribution of patch sizes, particularly the maximum patch size, was not driven by biotic interactions but rather by the individual size of the dominant plant species (as shown with CWH; Figure 4.4.b, Figure S 4.5.; see also von Hardenberg *et al.* 2010). In other words, more stressful conditions lead towards less and more isolated individuals, which form patches driven by the characteristic size of each plant species (see also von Hardenberg *et al.* 2010). Interestingly, the percentage of facilitated species was similar between PL-like and nonPL-like sites (average of 23.1%/24.9% in PL-like/nonPL-like sites) consistent with the widespread extension of facilitative interactions previously found in drylands (Flores and Jurado 2003, Valiente-Banuet et al. 2006, Soliveres and Maestre 2014). However, nurses (but not beneficiary plant species) were significantly smaller in the nonPL-like sites ($F(1,66) = 6.08$, $P = 0.02$), which likely hinders their ability to generate large patches when facilitating.

Insights for degradation indicators:

NonPL-like sites have in general a lower cover and higher aridity levels, and their patch-size distributions resemble truncated power laws. Also in these sites, PLR is explained mainly by features of their components (CWH) rather than biotic interactions and show a disconnection between aridity and total cover (Figure 4.4.). This does not necessarily mean that these sites are more degraded, although it is suggested by the different ecosystem dynamics (probably caused by degradation or imposed by environmental harshness). Regrettably, with the data we have, it is not

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possible to test whether deviations of power laws are a consequence of ecosystem degradation due to external stress. Further research efforts must be carried out to investigate the interplay between aridity and other stressors on the modulation of patch-size distributions in detail. We argue that in less-degraded systems patch-size distributions would be better described by simple biotic attributes, such as cover or the percentage of facilitative interactions (e.g., Kéfi et al. 2007b, Maestre and Escudero 2009), while in those in the proximity to a change in their dynamics are better described by the environmental stress and are driven by the features (i.e., CWH) of their individuals rather than by their interactions (Kéfi et al. 2007b, 2011, Scanlon et al. 2007). As a consequence, patch-size distributions reflect a response against abiotic drivers that other biotic attributes cannot reflect, thereby disentangling biotic and abiotic effects on the spatial organization of the ecosystem. Our results help to understand the response of patch size distributions to environmental conditions in drylands worldwide, and are in general agreement with both model predictions and previous field observations (Kéfi et al. 2007a, Maestre and Escudero 2009, Moreno de las Heras et al. 2011). Thus, this study helps on reconciling contradicting results regarding the suitability of either total cover or patch-size distributions as good indicators of ecosystem dynamics in drylands. Degraded or not, we show that the exponent decay of frequencies of large patch sizes (α) was always explained by biotic attributes such as total cover and community weighted mean plant height. These variables smoothed the decay in the frequency of larger patches (Figure 4.4. a and b). The disappearance of large patches as a consequence of increasing disturbance or aridity is, indeed, the main assumption behind the use of patch-size distributions as indicators of desertification. Our results indicate that patch-size distributions should not be used as indicators of degradation in systems dominated by relatively large woody individuals such as trees or shrubs, whose large patches are less likely to be divided by overgrazing or drought. Also special attention must be paid to processes linked to degradation that might change the woody community components when using patch-size distributions to track the ecosystem status (e.g. woody encroachment, see Van Auken 2000, Eldridge et al. 2011).

CONCLUSIONS

In this study, we analyzed 115 sites over the world in order to investigate the general typology and causal modulation of patch-size distributions in drylands. We could separate our sites in two types, according to their patch-size distribution characteristics, which identify a shift between biotic and abiotic controls of dryland plant communities. This study also revealed potential masking effects of ecosystem features such as relative woody cover and community weighted height on the decay in the frequency of larger patches. The latter limits the applicability of patch-size distributions as indicators of desertification in those sites dominated by large woody species. Our study provides strong empirical support to commonly held model assumptions largely untested in the field, such as: general fit of patch-size distributions to heavy tailed functions; the role of facilitation on the emergence of PL in less degraded sites, and the deviations of patch-size distributions from PL in harsh ecosystems. These results reconcile current controversy by indicating under which circumstances patch size distributions are likely to best perform as indicators of ecosystem status.

APPENDIX 1.1: ADDITIONAL ANALYSIS TO PROVE THE CONSISTENCY OF PATCH-SIZE DISTRIBUTIONS TYPES.

Because an important part of our study is dependent on the threshold found for patch size distribution types, we performed a sensitivity analyses to examine the consistency of this threshold to different methodologies. Both methods fit discontinuous regressions with a breaking point that changes its slope (known also as piecewise regressions), following equation S1.

$$\alpha = \alpha_{PL} \text{ iff } PLR \geq PLR_{thres}$$

$$\alpha = intcp - \beta * PLR \text{ iff } PLR < PLR_{thres} \quad \text{equation S 4.1}$$

In this equation, α_{PL} represents the slope (α) of the fit to a power law distribution, which is invariant as discussed above; PLR_{thres} represents the breaking point from which the effect of α and PLR shifts into 0; $intcp$ is the intercept of the linear regression of nonPL-like distributions and β is the slope of that same regression. Note that in this model the β parameter is not completely free, as it depends on the PLR_{thres} and α_{PL} values due to the discontinuity inherent of the equations. Thus, there are only three parameters to be calculated.

First, we used the iterative model selection procedure stated by Crawley (Crawley 2012), which look at different break points in a discontinuous model (see equation S1) and minimize the residual mean squared errors. Second, we used the package “segmented” in R (Muggeo 2008), which is specifically designed to look at piecewise regression for breaking points. Both approaches yielded similar values of the breaking points (0.58 and 0.62 ± 0.06 , respectively) to the ones we found originally (0.57). This variation in breakpoints make some sites to shift from PL-like to nonPL-like, but they are only a few of them (2 if considering Crawley approach, 10 if considering segmented package’s approach).

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Additional support for the division of patch size distribution types conducted is provided by the SEM analysis we performed after this classification and is discussed in the main manuscript Figure 4.4.

SUPPLEMENTARY FIGURES

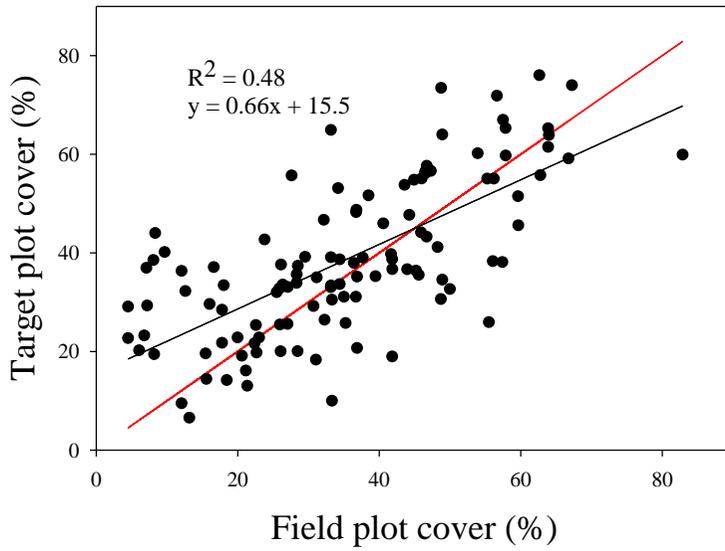


Figure S 4.1. Validation of patch classification

Relationship between the cover extracted from the images of target plots after visual classification ('Target plot cover') and the linear cover measured in the field ('Field plot cover'). Red line is the 1:1 line; black line is the linear regression. R^2 value and the resulting equation are displayed in the graph.

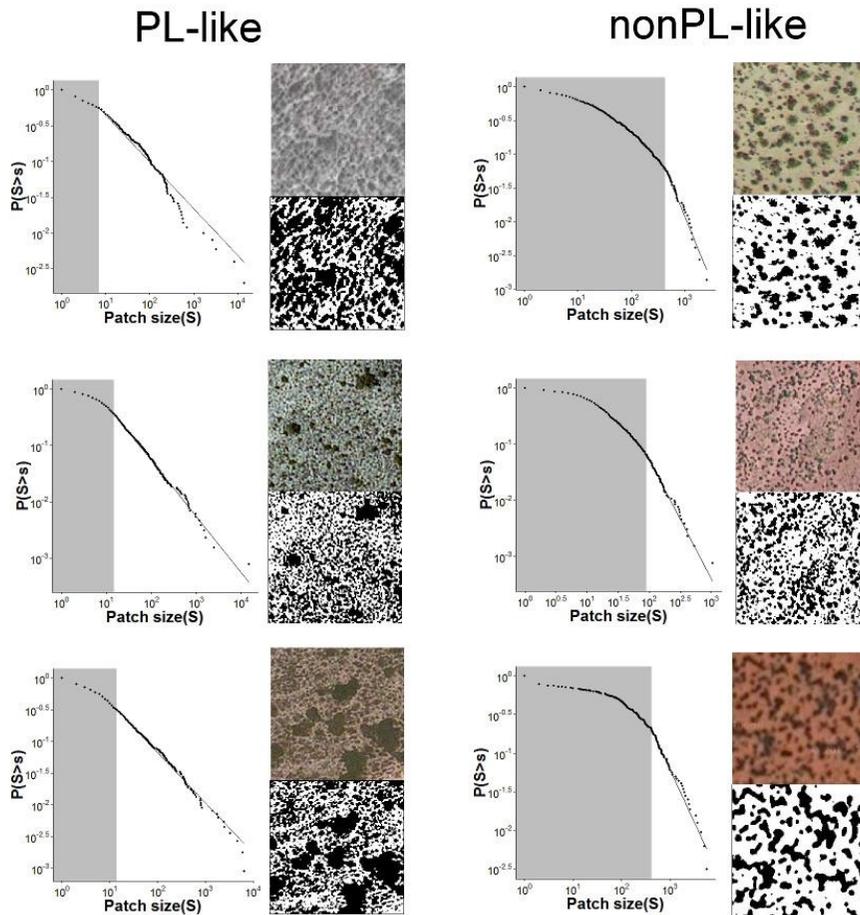


Figure S 4.2. Examples of patch-size distributions found in global drylands

Six examples of sites where the patch size distribution of vegetation either follows a power law (PL-like) or not (nonPL-like). The inversed cumulative distributions are shown (both axis are log-scaled). The original image and that resulting from its classification are displayed to the right of each distribution. The shaded area represents data with patch sizes lower than x_{min} (therefore not fitted to power law functions). The power law range (PLR) corresponds to the percentage of non-shaded area in each distribution. The black line is the fitted power law.

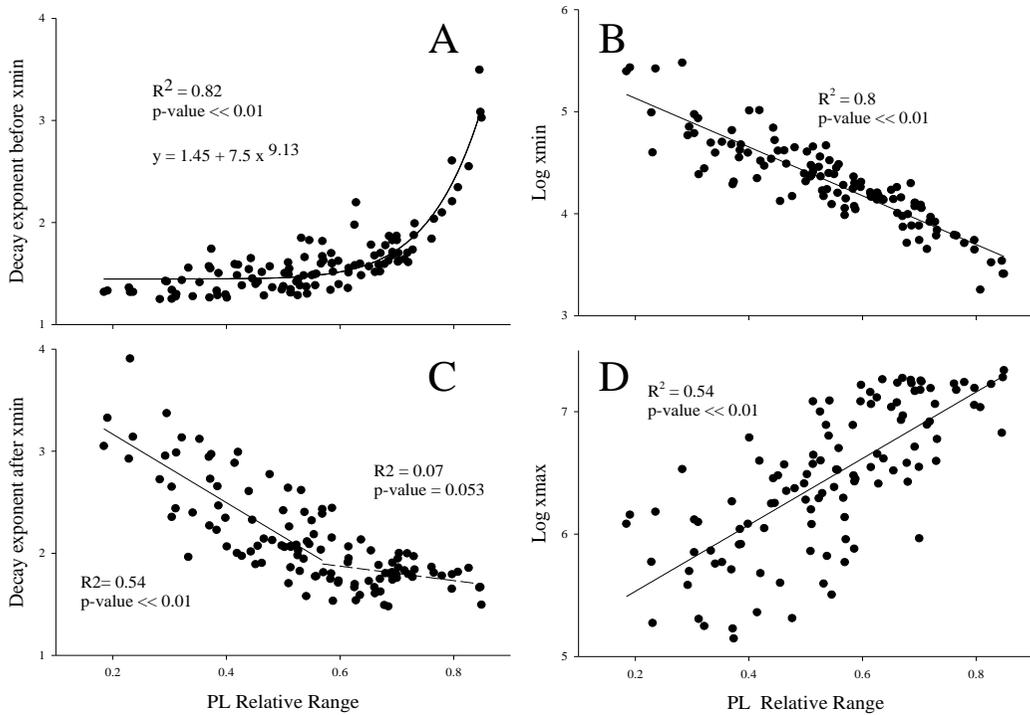


Figure S 4.3. Exploring patch-size distribution parameters.

Regressions between the percentage of orders of magnitude that follow a power law (PL relative range) and: the decay exponent of frequencies with patch sizes before (A) and after (B) the point of initialization of power law; the logarithm of the maximum patch size (Log x_{max} , D) and the logarithm of the point of initialization of power law (Log x_{min} , C). R^2 and p -value are displayed in each panel. In A panel, a power regression was performed. In B panel, two regressions were performed according to the discontinuity found in the data about $PLR = 0.57$ (see Figure 4.3.).

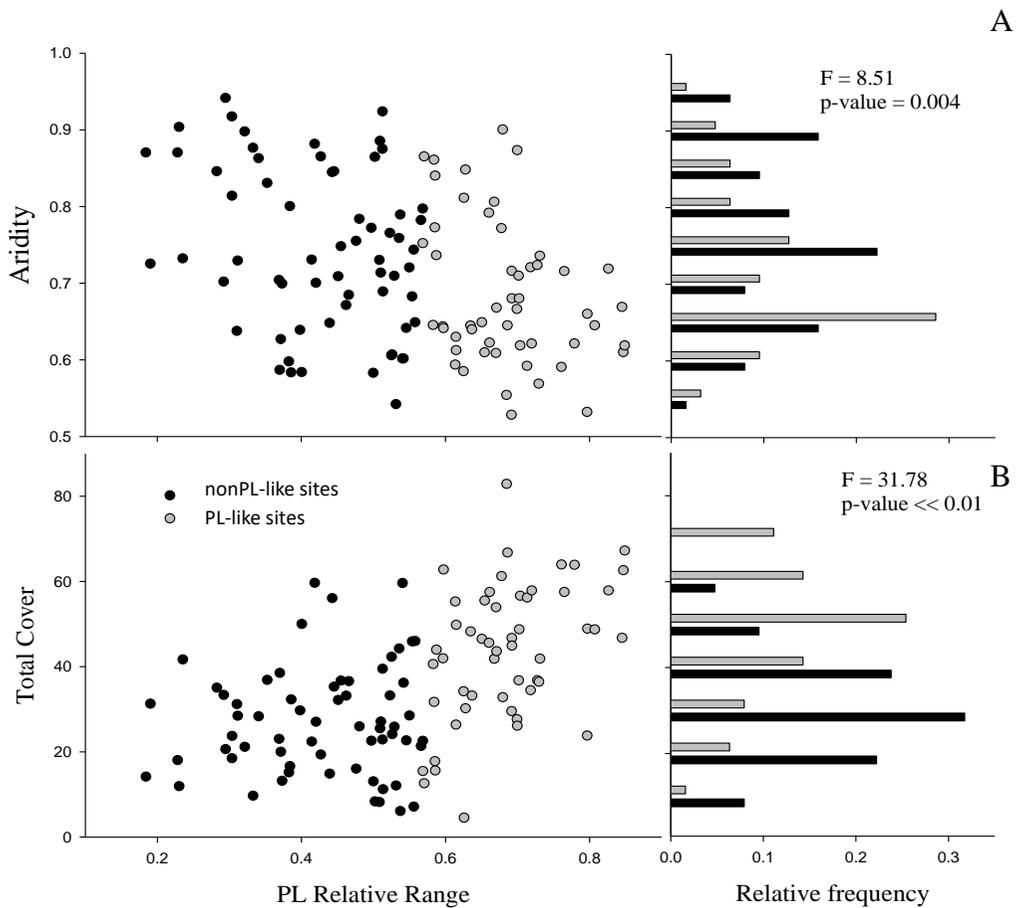


Figure S 4.4. . Relationships between types of patch size distribution (PL relative range) and aridity (A) or cover (B).

Relationship between the percentage of orders of magnitude that follow a power law (PL relative range) and aridity (A) and total cover (B). Grey indicates plots in the PL-like subset and black indicate plots in the non PL-like subset. The relative frequencies of aridity and total cover are displayed in the right part of each panel and Fischer Metric (F) and p-value corresponding to an ANOVA analysis confronting Aridity (A) and Total cover (B) between PL-like and non PL-like sites are displayed.

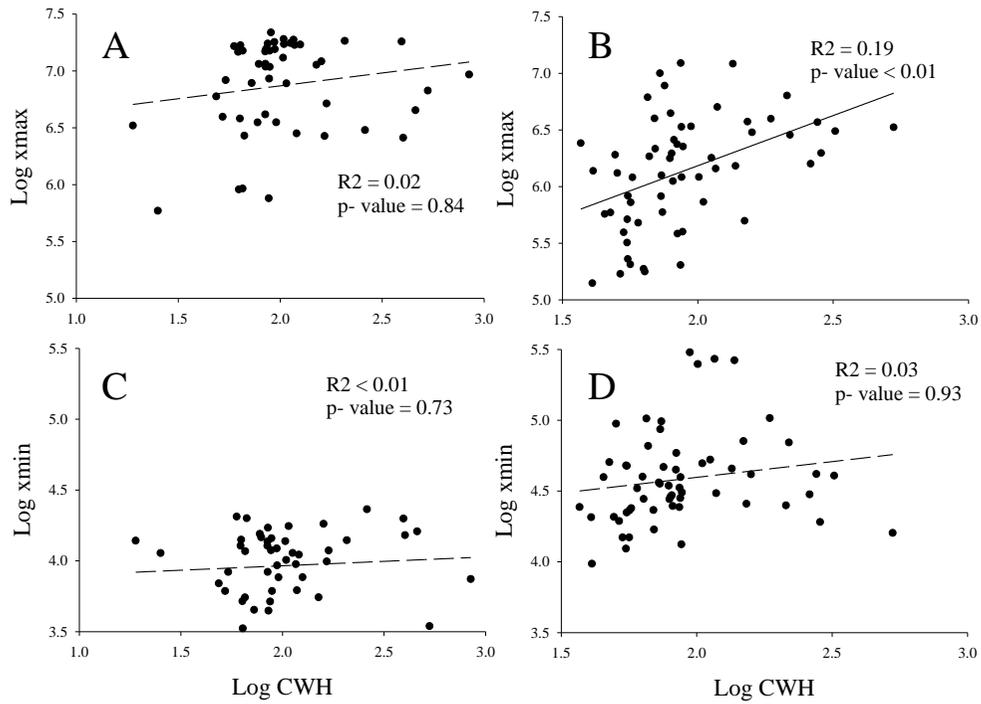
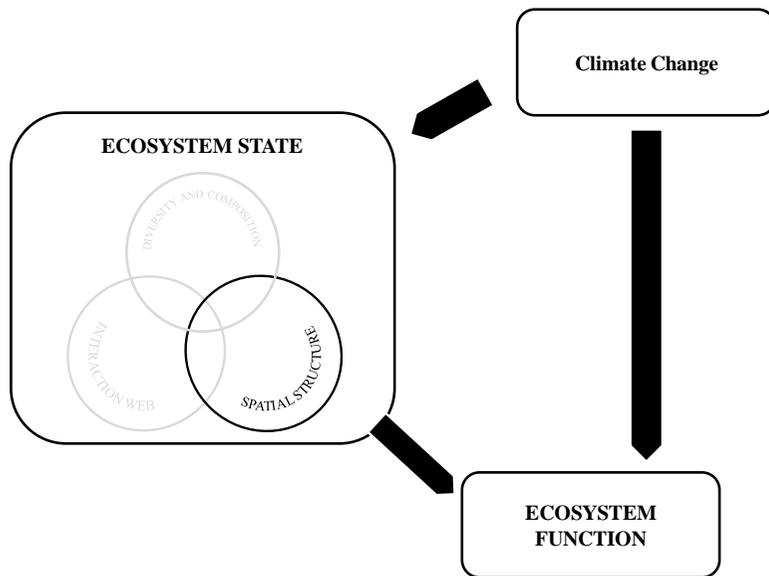


Figure S 4.5. Effect of community height on patch-size distribution parameters.

Regressions confronting the logarithm of community-weighted plant height (Log CWH) against: the logarithm of the patch size from which the power law initializes (Log xmin) in PL-like sites (C) and nonPL-like sites (D); the logarithm of the maximum patch size (Log xmax) in PL-like sites (A) and nonPL-like sites (B). R^2 and p-value from the resulting linear regression are displayed in each figure. Dashed lines indicate no significance and full lines indicate significance in the regression analysis.

CHAPTER 2

Plant spatial pattern identify alternative ecosystem multifunctionality states in global drylands



Miguel Berdugo, Sonia Kéfi, Santiago Soliveres, Fernando T. Maestre

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ABSTRACT

The response of drylands to environmental gradients can be abrupt rather than gradual. These shifts are largely unannounced and difficult to reverse once they happen, thus their prompt detection is of crucial importance. The distribution of vegetation patch sizes may indicate the proximity to these shifts, but their use is hampered by the lack of large-scale studies relating these distributions to the provision of multiple ecosystem functions (multifunctionality) and comparing them to other ecosystem attributes such as total plant cover. Here, we sampled 115 dryland ecosystems across the globe and related their vegetation attributes (cover and patch-size distributions) to multifunctionality. This latter variable followed a bimodal distribution across our sites, suggesting alternative states in the functioning of drylands. Although plant cover was the strongest predictor of multifunctionality when linear analyses were used, only patch-size distributions reflected the bimodality found in its distribution. Differences in the coupling between nutrient cycles and in the importance of self-organizing biotic processes characterized the two multifunctionality states observed. Our findings support the use of vegetation patterns as indicators of ecosystem functioning in drylands, and pave the way for developing effective strategies to monitor desertification processes.

Keywords: multifunctionality, spatial pattern, power law, alternative states, bistability

INTRODUCTION

The development of early warning signals to detect the onset of regime shifts in marine and terrestrial ecosystems has received increasing attention during the last decade (Scheffer et al. 2009, Dakos et al. 2012). Although rarely validated in natural ecosystems (Hirota et al. 2011), theoretical models suggest that drylands, which occupy over 41% of the Earth's surface and host 38% of the world's human population (Millenium Ecosystem Assessment 2005), are prone to exhibit regime shifts (e.g., from functional to desertified states, see Von Hardenberg et al., 2001, Rietkerk et al., 2004). The early detection of these regime shifts is particularly important in these ecosystems since desertification is a major environmental issue affecting more than 250 million people, especially in the developing world (Reynolds et al. 2007).

Dryland perennial vegetation commonly forms isolated patches interspersed with bare soil, whose distribution of sizes is often characterized by heavy-tail distributions (i.e., there are many small and a few very large patches Scanlon et al. 2007, Lin et al. 2010, Kéfi et al. 2011, Moreno de las Heras et al. 2011). Such heavy-tail distributions commonly fit a power law function, and have been suggested to be a consequence of plant-plant interactions and plant-soil feedbacks (Von Hardenberg et al. 2001, Kéfi et al. 2011). Mathematical models predict that patch-size distributions would deviate from a pure power law function with increasing external disturbances (Kéfi et al. 2007a, 2011). Thus, these deviations could indicate that the ecosystem is close to a regime shift, leading to drastic declines in its functioning (Kéfi et al. 2007a, 2011, Manor and Shnerb 2008a). However, we lack empirical support regarding the ability of patch-size distributions to reflect loss of ecosystem functioning in drylands. Most attempts to evaluate patch-size distributions in the field have spanned a limited range of sites and environmental conditions (Kéfi et al. 2007a, Maestre and Escudero 2009, Lin et al. 2010). Additionally, few studies have linked patch-size distributions to ecosystem functioning or have compared their performance as indicators of ecosystem functioning with attributes such as vegetation cover (Maestre and Escudero 2009, Kéfi et al. 2010a, Bestelmeyer et al. 2013). These knowledge gaps raise doubts about which of the currently recommended management and monitoring tools (e.g. plant cover, Zurlini et al., 2014, or patch-size distributions) are more suitable to detect losses in ecosystem functioning such as those caused by desertification

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(Cowie et al. 2011). We used the metric developed in the previous chapter called power law relative range (PLR hereafter), which can be used to characterize any heavy-tailed distribution and its adjustment to a power law function. In the previous chapter, we identified two main types of patch-size distributions in our data, based on thresholds in their shape that compromise the scale-invariance of the distributions (a fundamental property of power law functions). We found that there are two types of patch-size distributions when analyzed according to their relative fitting to power laws and that were driven by abiotic/biotic drivers respectively.

Here, we used remote sensing and field data from a survey conducted in 115 drylands spanning four continents and measured vegetation cover, patch size distribution and the ability of the ecosystem to supply several functions at the same time (multifunctionality, see Hector and Bagchi 2007, Isbell et al. 2011, Maestre et al. 2012a), calculated as the average Z score of 16 soil variables (functions hereafter) related to carbon (C), nitrogen (N) and phosphorous (P) cycling (see Methods). However, ecosystem attributes do not always vary linearly along environmental gradients (Scheffer et al. 2009, Suding and Hobbs 2009). Indeed, drylands are iconic examples of ecosystems whose response to environmental gradients can be abrupt rather than gradual, thereby shifting from one ecosystem state to another (Scheffer et al. 2001, Rietkerk et al. 2004, Suding et al. 2004). Therefore, in a second step, we tested the possible occurrence of different stable states in multifunctionality in our dataset as well as the variation of patch-size distributions, cover and multifunctionality along aridity gradients.

MATERIAL AND METHODS

Study sites and data collection

We used the database described in Maestre et al. (Maestre et al. 2012a), which contains vegetation and soil data of 224 drylands, as well as data from six additional dryland sites surveyed during 2013 in Botswana using the same methodology. From these sites, we retained for this study those from which information of patch-size distributions were obtained in the previous chapter. The 115 sites used are grasslands or shrublands with discontinuous perennial plant

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cover and are located in 13 countries and differ widely in their abiotic (elevation, temperature and precipitation) and biotic (cover and number of species) attributes.

At each site, we established a 30 m × 30 m plot representative of the vegetation present in that area and estimated plant cover using the line intercept method (Tonway and Hindley 2004, see more details in Maestre et al. 2012a, Delgado-Baquerizo et al. 2013). We also took five soil cores (0-7 cm depth) in areas devoid of perennial vegetation during the dry season. Finally, we obtained values of the aridity index (AI, precipitation/potential evapotranspiration) from (Zomer et al. 2006), who used the data interpolations provided by Worldclim (Hijmans et al. 2005). To facilitate the interpretation of the results, we calculated the aridity level of each site as $1 - AI$ (Delgado-Baquerizo et al. 2013), so higher values of this aridity level indicate drier conditions.

It must be noted that we use a space-by-time substitution approach, which has been shown to reflect changes in biotic attributes and ecosystem functions such as those studied here (Blois et al. 2013) but should not be considered as evidence of more dynamic processes such as desertification.

Assessing multifunctionality

We measured 16 soil variables related to the C (organic C, β -glucosidase activity, pentoses, hexoses, aromatic compounds, and phenols), N (nitrate, ammonium, total N, potential N transformation rate, amino acids and proteins) and P (available P, phosphatase activity, inorganic P and total P) cycles. These variables are ecosystem functions (*sensu* (Reiss et al. 2009), e.g. potential N transformation rate) or variables related to key properties/processes (*sensu* Jax 2010, e.g., organic C, total N and soil enzymes). These variables have been used in previous studies of ecosystem functioning and multifunctionality (Hector and Bagchi 2007, Gamfeldt et al. 2008, Maestre et al. 2010, Orwin et al. 2010, Zavaleta et al. 2010), and are considered to be critical determinants of soil fertility and ecosystem functioning in natural and semi-natural drylands (see Whitford 2002 for a review). Most of these functions are also considered to be supporting ecosystem services, as other types of ecosystem services, such as the production of plant biomass and livestock, depend on them (Millenium Ecosystem Assessment 2005, Balvanera et al. 2006, Isbell et al. 2011). Additionally, variables such as those used here have been recommended to study long-term ecosystem changes and resource collapses because they have

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long turnover times (Reynolds et al. 2007) and, therefore, are less sensitive to inter-annual variations in climate. For simplicity, all the soil variables measured are called ‘functions’ (Gamfeldt et al. 2008). After field collection, the soil samples were sieved (2 mm mesh), air-dried for one month and stored for laboratory analyses (Maestre et al. 2012a, Delgado-Baquerizo et al. 2013). To standardize soil analyses, dried soil samples from all the countries were shipped to Spain, where they were analyzed following the same protocols and in the same laboratories (described in Delgado-Baquerizo et al. 2013 and Maestre et al. 2012a, see also Appendix 2.1).

We calculated multifunctionality using the M index of Maestre et al. (Maestre et al. 2012a), obtained as the average Z-score across functions. This index has good statistical properties (Maestre et al. 2012a) and is increasingly used in multifunctionality studies (Quero et al. 2013, Bradford et al. 2014, Pendleton et al. 2014, Wagg et al. 2014, Lefcheck et al. 2015, Valencia et al. 2015). This index is an averaging method and attempts to summarize multifunctionality so that high values of M mean high values of many of, but necessarily all, the functions included. Thus, high values of all our functions have been associated with more functional ecosystems. Since the latter may depend on the ecosystem or function considered, we also report results on each individual function to ease interpretation of our findings. It must be noted that M cannot distinguish between (i) two functions having similar values and (ii) one function having high values and other function having low values (suggesting trade-offs between two given functions, Byrnes et al. 2014). To account for this issue, we also estimated multifunctionality using the multiple-threshold approach of (Byrnes et al. 2014), which evaluates the number of functions that simultaneously exceed multiple critical thresholds calculated as a proportion from the top 5% performing sites for each function.

Characterising path-size distributions

We used the power law relative range method (see previous chapter) to extract a continuous metric of the deviations from power law fitting of the patch size distributions. We directly used the dataset obtained in the previous chapter. There, we classified Google Earth and Virtual Maps images of the sites of study by using MATLAB scripts able to classify vegetation cover. We then fitted the patches of vegetation extracted from the images to power law functions and obtained x_{\min} and

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α parameters using MATLAB script from (Clauset et al. 2009). We derived the power law relative range metric by using the function:

$$PLR = 1 - \frac{(\log_{10}[x_{min}] - \log_{10}[x_{lowest}])}{(\log_{10}[x_{max}] - \log_{10}[x_{lowest}])} \quad \text{equation 5.1}$$

The obtained metric varies from 0 to 1 describing the proportion of patch sizes order that fits a power law. Such metric was found to correlate with the relative fitting to power law functions as well as with the shape of the patch-size distribution (values close to 0 indicate curved-like distributions whereas values close to one indicate power law-like distributions). Also this metric was found to distinguish two types of distributions in drylands. The one called PL-like had PLR values greater than 0.57 and was driven by biotic factors including facilitation and total cover. Non PL-like distribution had PLR values lower than 0.57 and were driven by abiotic factors (aridity) and the height of the dominant species.

Statistical analyses

Relationships between PLR, cover and multifunctionality

Both PLR and cover can be good indicators of changes in ecosystem functioning (Maestre and Escudero 2009, Bestelmeyer et al. 2013). To test which one is a better indicator of multifunctionality in our data, we first performed a simple correlation between all functions and M versus both PLR and cover separately; then we calculated a partial correlation for each function versus PLR controlling by cover.

Bimodality in multifunctionality

We tested for the possible occurrence of several multifunctionality states based on the frequency of the multifunctionality values in our data (assuming the most frequent to be more stable Livina and Lenton 2007, Hirota et al. 2011). To test whether multifunctionality showed multiple modes in the sites studied, we used Gaussian mixture models analysis (McLachlan and Peel 2004). This technique calculates the Bayesian (BIC) and Akaike Information Criterion (AIC) metrics for either one or two mode distributions fitted to the data. The minimum AIC/BIC value corresponds to the most likely number of modes (i.e., Gaussian distributions

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within the data) of the distribution. We performed this analysis by using the *gmdistribution.fit* function in Matlab.

If we consider the observable system to be dynamically coherent (i.e., to tend in time always into a steady state), a collection of snapshots of this system will reveal less frequent values of non-stable states, while values close to stability will appear more often (Livina and Lenton 2007, Hirota et al. 2011). This implies that a surrogate of the dynamic potential of the system (interpretable as the “odds” of change of the system as a function of the state variable) might be derived directly from the probability density function of the variable of interest (i.e., multifunctionality), as:

$$U' = -\frac{\sigma^2}{2} \log(PDF) \quad \text{equation 5.2}$$

where PDF is the Probability Density Function empirically derived from the dataset. By calculating the scaled potential (U'/σ^2), we do not need to estimate the level of noise of the system (σ^2). We obtained the PDF by using the Matlab function *ksdensity*, with a standard bandwidth ($h = 1.06 \text{ s}/n^{0.2}$ with s the standard deviation of the data and n the number of data points). Then, we used equation 2 to obtain the potential, which is shown in Figure 5.1a. This potential represents an analogy of dynamical stability in the system, in which local minima are often interpreted as stable states (see details in Appendix 2.2).

To test the robustness of our results regarding the two alternative states in multifunctionality, we performed three additional sensitivity analyses (Appendix 2.3 and Figure S 5.1). These analyses aimed to test that the bimodal pattern of multifunctionality was: (i) consistent regardless of the approach used for measuring multifunctionality, (ii) not a consequence of the subset of sites for which we could find good quality images, and (iii) not confounded by the distribution of aridity or any other predictor.

Structure of the relationships between functions in each multifunctionality state

To better understand the mechanisms driving the two alternative states in ecosystem multifunctionality found, we assessed the relationship between each individual function within the two multifunctionality states, as well as the

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relationships between functions and multifunctionality state. We expected tighter relationships between functions in the high multifunctionality state, as soil functions in high functional systems usually covariate strongly with each other (Delgado-Baquerizo et al. 2013). We also expected a differential role of functions associated to each major nutrient cycle (C, N and P) as drivers of ecosystem multifunctionality due to the changes in nutrient stoichiometry of soils observed in disturbed or arid systems (Delgado-Baquerizo et al. 2013, Wang et al. 2014). This occurs because different soil nutrients usually relate to similar metabolic pathways (e.g., N and C are biotically driven whereas P is mostly driven by abiotic processes McGill and Cole 1981, Finzi et al. 2011). A switch in the control of a specific soil function over the others can be induced by changing the limiting factors in these soil processes (Vitousek et al. 2010) or by delimiting biogeochemical cycles to episodic water inputs (Austin et al. 2004). In particular, phosphorus and nitrogen/carbon nutrient pools may uncouple under arid conditions, exhibiting a shift in the dominating factors from carbon/nitrogen in low aridity (biotically controlled) sites to phosphorus in high aridity (abiotically controlled) sites (Delgado-Baquerizo et al. 2013).

We assessed the relationship between each individual function, and between them and our overall multifunctionality metric in each one of the two multifunctionality states found, using linear correlations between all these variables. This allowed us to examine the most important (linked) components of ecosystem functioning and their relative contribution to the variation of M in the two multifunctionality states.

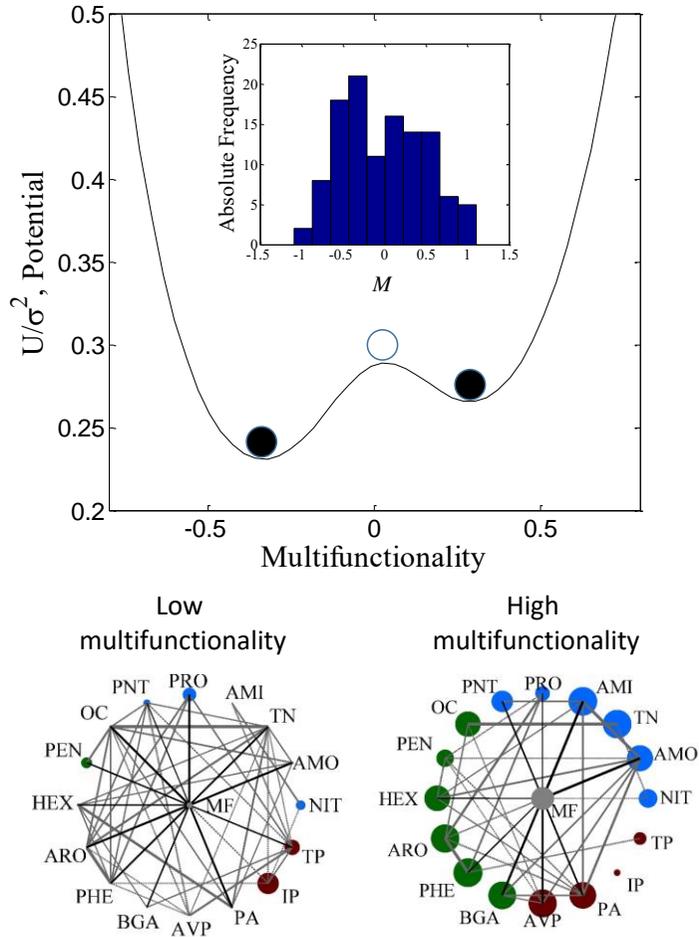


Figure 5.1. Alternative states in drylands' multifunctionality.

a) Stability landscape of the studied ecosystems as a function of multifunctionality. Grey balls represent the local minima ('stable' states) and the white ball the local maximum ('unstable' states). The histogram in the insert shows multifunctionality values and the two distributions fitted based on the Gaussian mixture analysis. The stability landscape is derived from this histogram. b) Relationships between the different functions (circles) measured in low and high multifunctionality states. Functions belonging to the nitrogen (blue), carbon (green) and phosphorous (red) cycles and the multifunctionality index (grey) are shown. The size of circles is proportional to their Z score. Lines connecting functions represent significant relationships between them, and their size is proportional to their Pearson correlation coefficient. PRO: proteins; AMI: amino acids; NIT: nitrates; TN: total nitrogen; OC: organic carbon; M: multifunctionality; TP: total phosphorous; IP: inorganic phosphorous; PA: phosphatase activity; AVP: available phosphorous; BGA: beta-glucosidase activity; ARO: aromatic compounds; PNT: nitrogen transformation rate; PHE: phenols; HEX: hexoses; PEN: pentoses; AMO: ammonium.

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Calculating stability landscapes of multifunctionality, PLR and cover

To investigate to what extent plant cover and PLR were related to the bimodal distribution of multifunctionality observed, we derived a map depicting the trend in the number and value of estimated alternative states (local minima as in Figure 5.1a) along the aridity gradient studied. By doing so we evaluated the response of plant cover and patch-size distributions to changes in aridity, and compared their responses to the two multifunctionality alternative states observed. We first investigated if aridity was the trigger for such discontinuous changes in multifunctionality by sequentially obtaining the potentials of multifunctionality throughout the transformation of its probability density functions into potential dynamical curves (Livina and Lenton 2007). To do so, we took the 40 less arid sites and plotted their dynamical energy potential curve. Then we sequentially changed the subset of plots by adding the next more arid plot and discarding the less arid one (total number of transits = 76). Our analyses show how the potential of multifunctionality changes throughout aridity in a tri-dimensional space, which is a reconstruction of the theoretical potential landscape through aridity. If this tri-dimensional space is seen from above in 2-D we obtain Figure 5.3, which represents a map of the expected trends of the alternative states through aridity. This figure is a reconstruction of the way multifunctionality would change along an increasing aridity gradient if it was constrained to move only through stable (understood as local minima in the derived potential) states. We conducted the same analyses using PLR and cover, which allowed us to evaluate nonlinear and discontinuous trends in these relationships.

Testing the association between the types of patch-size distribution and the multifunctionality states

We wanted to assess whether the two major classes of patch-size distributions identified (PL-like and nonPL-like sites) were related to the multifunctionality (M) states found. To do so we first classified our sites according to these states, considering high and low functional sites those in which M was higher and lower than the unstable state ($M \approx -0.06$; understood as the maximum in the potential between the two alternative states, see Figure 5.1a), respectively. Second, we performed a Chi-square test using SPSS version 20 (IBM Corp. in Armonk, NY) between patch size distribution types (PL-like /nonPL-like) and multifunctionality types (high/low multifunctionality).

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Both patch-size distribution types and multifunctionality states are influenced by aridity. As such, the association between these variables could be confounded by their common response to aridity. To evaluate the association between patch size distribution and multifunctionality types along the different levels of aridity studied, we performed the Chi-square tests described above (association between High/low multifunctionality and PL-like /nonPL-like types of patch size distributions), but across a moving window through aridity. To do so, we first ordered the sites from low to high aridity values; we then took a subset of the 40 less arid sites and performed the Chi-square test. This step was repeated iteratively by sequentially discarding the first site (less arid) and adding the next more arid site through all our study sites.

RESULTS

Total plant cover was a better linear predictor of multifunctionality, M , than patch-size distributions (Table S 5.1.). Results using multiple threshold approach were very similar to those obtained using M (Figure S 5.2.), and are therefore not further discussed. However, when we tested for the possible occurrence of several multifunctionality states based on the frequency of the multifunctionality values in our data, this analysis revealed a bimodal distribution of multifunctionality values in our sites (ΔAIC with one mode vs two modes ~ 7.89 , Figure 5.1), which can be interpreted as the existence of two multifunctionality alternative states in global drylands (Hirota et al. 2011). These results were robust to the approach used to estimate multifunctionality (Figure S 5.3. and Figure S 5.4.) and to the number of sites considered (Appendix 2.3), and were not confounded by the effects of aridity on both PLR and multifunctionality (Figure S 5.5). Importantly, the relationship between cover and multifunctionality changed when both multifunctionality states were taken into account (Figure 5.2a).

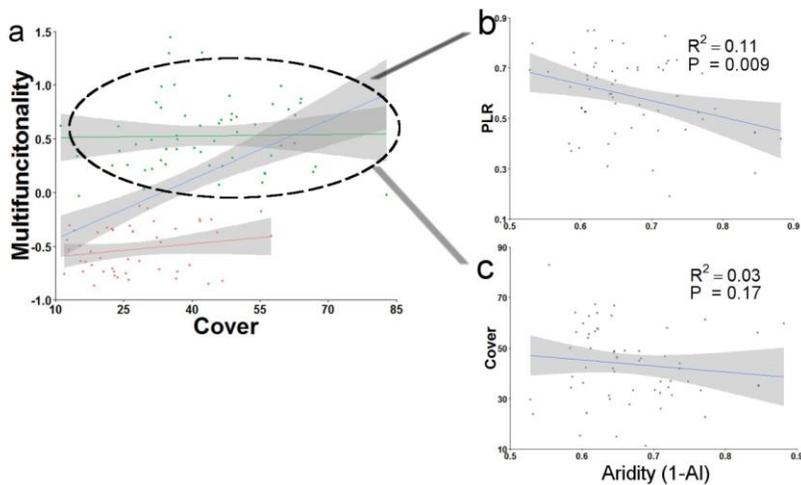


Figure 5.2. Varying relationships between plant cover, patch-size distributions, multifunctionality and aridity.

Relationship between cover and multifunctionality for all our study sites (blue line, $F=43.3$, $P<0.001$) and for sites from high (green line, $F=0.26$, $P=0.61$) and low (red line, $F=4.8$, $P=0.03$) multifunctionality states (a). The right panels show the relationships between aridity (1 – aridity index, AI) and both the power law relative range (PLR, b) and cover (TCT, c) in the sites from the high multifunctionality state (surrounded by a ellipse in panel a, $N = 53$). The shaded areas indicate the confidence intervals of the linear regressions.

Multifunctionality potential landscapes illustrates a possible regime shift from one alternative state to another when aridity ranges between 0.7-0.8; in this range of aridity values both states coexist (Figure 5.3). Cover and PLR showed only one mode throughout their potential landscapes (Figure 5.3). However, while cover smoothly decreased with aridity, PLR showed an abrupt decrease occurring close to the point of co-occurrence of the two multifunctionality states observed (Figure 5.3). This drop in PLR concurs with the shift in patch-size distributions observed from PL-like to non PL-like sites, and reflects contrasting drivers of plant spatial patterns (previous chapter). Indeed, the type of patch-size distribution was significantly associated with the two multifunctionality states observed ($\chi^2 = 6.64$, $P = 0.01$), and this association was even stronger at those aridity levels in which the two multifunctionality states co-occurred (Figure S 5.6). Moreover, since these ranges of aridity (0.65-0.8) are the ones in which aridity related more poorly to multifunctionality, we can exclude any confounding effect from aridity on the relationship between patch size distribution and multifunctionality.

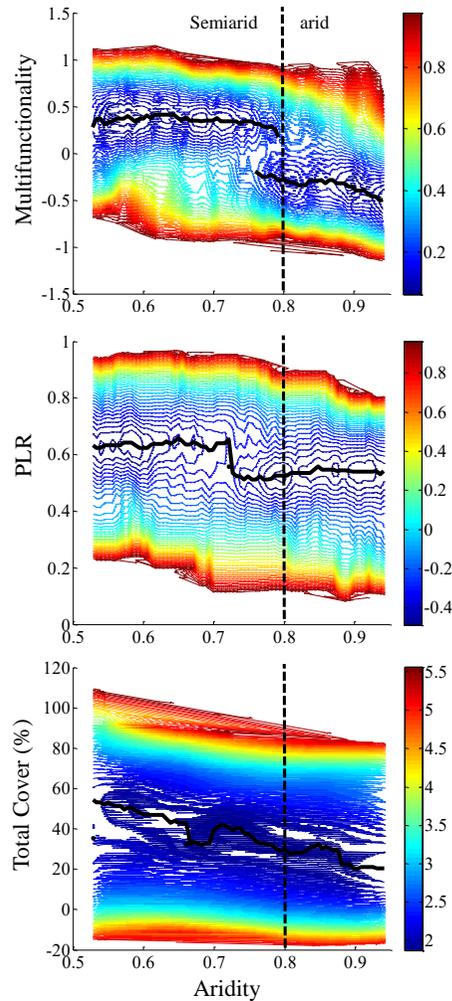


Figure 5.3. Relationship between aridity and plant cover, patch-size distributions and multifunctionality.

Variation of the ‘stable’ states (i.e. local minima of the stability landscape; see Figure 5.1. a, black line) along the aridity gradient studied for multifunctionality (a), the power law relative range (b) and cover (c). AI = aridity index (annual precipitation / annual evapotranspiration). Contour lines represent the estimated potential energy from which the ‘stable’ states are derived as local minima (as shown in Figure 5.1. a). The vertical line marks the limit between semiarid and arid sites.

To further understand the mechanisms driving the two multifunctionality states observed, we calculated the correlations between all pairs of ecosystem functions examined. In the high multifunctionality sites, these functions were strongly

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correlated, and multifunctionality was co-driven by many of them (Figure 5.1 b). In the low multifunctionality sites, organic C and total N contents were the main drivers of multifunctionality, and functions were loosely linked to each other (Figure 5.1 b).

DISCUSSION

We analyzed for the first time the relationship between plant cover, patch-size distributions and ecosystem multifunctionality across many habitats and biogeographic regions. Our results show that plant cover is the best predictor of linear changes in multifunctionality but that only patch-size distributions relate to the two contrasting states in multifunctionality found in global drylands. The contrasting importance of biotic and abiotic drivers of the two types of patch size distributions matched with the two multifunctionality states found. This suggests a shift from systems controlled by biotic interactions to abiotically controlled systems when aridity reaches high levels. Overall, our results highlight the suitability of patch-size distributions (particularly changes from those fitting to a power law vs those that do not) as markers of functional ecosystem types in drylands.

We found that, when using linear statistical models, cover explained multifunctionality metrics better than the shape of patch size distributions (measured as PLR), extending previous findings (Maestre and Escudero 2009, Bestelmeyer et al. 2013) to drylands worldwide. However, the bimodal nature of multifunctionality found in our study (Figure 5.1a) calls for the search of metrics able to detect these alternative states, whose existence may influence the relationship between ecosystem functioning and monitoring metrics such as vegetation cover or patch size distributions. Indeed, cover was associated to multifunctionality in the low but not in the high multifunctionality state (Figure 5.2a), which casts doubts about the suitability of plant cover to reflect alternative functional states. The fact that PLR exhibited an abrupt drop in the range of aridity values where the two multifunctionality states co-occur (Figure 5.3), together with the association between the type of patch size distribution and the multifunctionality states (Figure S 5.6), points that vegetation spatial organization might be reflecting multifunctionality states. Changes in patch-size distributions

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are not only related to the different drivers of ecosystem dynamics, but also indicate a spatial reorganization of the existing plant cover. This spatial reorganization is directly linked to processes influencing ecosystem functioning in drylands, such as soil erosion (Mayor et al. 2013), and can reflect important variations in the structure of plant communities unrelated to variations in vegetation cover. For example, a replacement in the dominant plant functional traits (Díaz et al. 2007) can affect nutrient cycling and the patch-size distribution via litter contributions to the soil and species interactions (Cornwell and Ackerly 2009); however, these functional changes might not be associated to changes in plant cover. The inclusion of community composition in catastrophic shift theory might bring new insights about the origin of this shift. We also found that, for the sites within the high multifunctionality state, PLR was negatively related with aridity, whereas cover did not respond to increases in aridity in these cases (Figure 5.2b and c). This result further supports the potential of patch-size distributions to anticipate discontinuous changes in ecosystem functioning if the latter are triggered by increases in aridity or related disturbances (e.g, higher sensitivity to grazing, changes in the importance of fires). Regardless of the mechanisms involved, our results clearly show that while plant cover is the best linear predictor of multifunctionality in drylands, patch-size distributions are better at identifying alternative states of this variable.

Contrasting correlation patterns of soil nutrients in low and high multifunctionality states observed allowed us to gain insights in the functional changes that occur between them. In low multifunctionality sites, total organic C and total N were the main drivers of the rest of soil nutrients and multifunctionality itself (Figure 5.1b). As changes in soil organic C and total N contents in drylands are largely driven by the activity and abundance of plants (Delgado-Baquerizo et al. 2013, Wang et al. 2014), our results suggest an increasing importance of biotic components as drivers of biogeochemical cycling in the low multifunctionality sites (Delgado-Baquerizo et al. 2013). Indeed, in the high multifunctionality sites, organic C and total N may be less limiting due to the relatively high inputs from biological activity, in accordance to the biotic control observed in their associated PL-like patch-size distributions. Therefore, non-biotically driven functions, such as available P, become important drivers of functioning at this high multifunctionality states. The aridity value at which both multifunctionality states co-occur is around 0.7 (range 0.6-0.8; Figure 5.3), which matches a shift from positive to negative net

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N inputs into the soil found in Chinese drylands (Wang et al. 2014). Our findings extend this result by showing that discontinuities in multifunctionality states might be related to the uncoupling of processes related to the cycling of major elements, and that these discontinuities are reflected by variations in plant spatial patterns.

CONCLUSIONS

Our results have important implications for the study of dryland responses to climate change. They suggest that ecosystems with aridity levels between 0.6 and 0.8 (i.e. in the transition zone between semi-arid and arid drylands) may undergo different multifunctionality states, with large contrasts in soil fertility, nutrient capture and cycling. A key result of our study is that these states are associated to different distributions of vegetation patch sizes, which are related to important changes in the way dryland ecosystems are organized. By providing the first empirical links between plant spatial patterns and multifunctionality in global drylands, our study suggests the use of spatial patterns as indicators of drastic variations in ecosystem functioning (Kéfi et al. 2007a, 2011, Manor and Shnerb 2008a). Additional studies evaluating temporal trends in both the spatial structure of vegetation and multifunctionality are needed to further investigate the role of patch-size distributions as early warning signals of regime shifts in terrestrial ecosystems. Our results pave the way for developing effective indicators to detect such shifts, and new restoration tools considering the nonlinear nature of multifunctionality in drylands.

APPENDIX 2.1: LABORATORY ANALYSIS OF SOIL VARIABLES.

We obtained data for 16 soil variables related to carbon (C), nitrogen (N) and phosphorous (P) cycling. As carbon cycling functions we measured Organic Carbon, Pentoses, Hexoses Aromatic compounds, Phenols and beta glucosidase activity. As N functions we measured: total nitrogen, amonium, nitrate, aminoacids, proteins and potential nitrogen transformation rate. As P cycling surrogates we took: total phosphorous, inorganic phosphorous, phosphatase activity and available phosphorous. These functions are either real functions or variables related to key properties/processes which has been used in previous studies of ecosystem functioning as critical determinants of soil fertility, nutrient cycling and biological productivity.

Organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid (Anderson and Ingram 1994). Total N was obtained using a CN analyzer (Leco CHN628 Series, Leco Corporation, St Joseph, MI, USA). Available P was measured following a 0.5M NaHCO₃ (pH: 8.5) extraction (Olsen and Sommers 1982). Soil extracts in a ratio of 1:5 were shaken in a reciprocal shaker at 200 rpm for 2 h. An aliquot of the centrifuged extract was used to the colorimetric determination of P inorganic available (PO₄⁻³), based on the reaction with ammonium molybdate and development of the “Molybdenum Blue” color (Bray and Kurtz 1945); the pH of the extracts was adjusted with 0.1N HCl when necessary. Phosphatase activity was measured by determination of the amount of p-nitrophenol (PNF) released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate p-nitrophenyl phosphate in MUB buffer (pH 6.5; (Tabatabai and Bremner 1969)). The activity of β-glucosidase was assayed following the procedure for phosphatase, but using p-nitrophenyl-β-Dglucopyranoside as substrate and Trishydroxymethyl aminomethane instead of NaOH when preparing the buffer (Tabatabai 1982). The remaining soil variables were measured from K₂SO₄ 0.5 M soil extracts in a ratio 1:5. Soil extracts were shaken in an orbital shaker at 200 rpm for 1 h at 20°C and filtered to pass a 0.45-µm Millipore filter (Jones and Willett 2006). The filtered extract was kept at 2 °C until colorimetric analyses, which were conducted within the 24 h following the extraction. Sub-samples of each extract were taken for measurements of aromatic compounds, phenols, pentoses, hexoses, proteins and aminoacids according to Chantigny et al. (Chantigny et al. 2006). Ammonium (NH₄⁺-N) and nitrate (NO₃⁻-

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N) concentrations were also measured for each K_2SO_4 extract subsample. Ammonium concentration was directly estimated by the indophenol blue method using a microplate reader (Sims et al. 1995). Nitrate was first reduced to NH_4^+ -N with Devarda alloy, and its concentration was determined by the indophenol blue method. Nitrate concentration in the extracts was calculated as the difference between Devarda-incubated and un-incubated samples. Potential N transformation rate was measured by determination of total K_2SO_4 -extractable N before and after incubation in the laboratory at 80% of field water holding capacity and 30°C for 14 days (Delgado-Baquerizo and Gallardo 2011).

APPENDIX 2.2: ADDITIONAL INFORMATION ON THE MEANING OF THE POTENTIAL FUNCTION

Stability in a physical system is often represented by the potential energy function of such system. This function represents the energy of a state variable, and, in a dynamical system, we may interpret it as the “odds to change” of that variable (Strogatz 2014). Local minima in potential functions represent dynamically “stable” states of the variable, whereas the other values will tend towards a stable state according to the shape of the potential (moving always from high potential values to lower values Strogatz 2014).

We consider that there is a generic underlying stochastic system driven dynamically, such that a potential function is yielded in the form:

$$dz = -U(z)dt + \sigma dW \quad \text{equation S 5.1}$$

where z corresponds to the state variable (multifunctionality), U is the potential function representing the dynamical energy of the system as a function of its own state, σ is the noise level and dW is a noise term emerging from a Wiener process. The Fokker-Planck equation connects the probability density to the potential of the underlying model, so that the potential might be derived as (Livina and Lenton 2007):

$$U' = -\frac{\sigma^2}{2} \log(PDF) \quad \text{equation S 5.2}$$

APPENDIX 2.3: SENSITIVITY ANALYSIS OF BIMODALITY IN MULTIFUNCTIONALITY.

To test the robustness of the alternative states in multifunctionality found, we performed three additional sensitivity analyses. With them we aimed to test whether the bimodal pattern of multifunctionality was: (i) consistent regardless of the approach used for measuring multifunctionality, (ii) not a consequence of the subset of sites for which we could find good quality images and (iii) not confounded by the distribution of a key driver of multifunctionality such as aridity.

Multifunctionality can be measured either by analyzing separate functions independently, with the averaging approach described above, or by evaluating the number of functions that reach single (Zavaleta et al. 2010) or multiple (Byrnes et al. 2014) thresholds. We assessed the robustness of our findings to all these different approaches available to estimate multifunctionality. First, we performed Gaussian mixture models on all the functions separately (normalized as Z-scores to ease interpretation of the results, Figure S 5.3). Second, we transformed the Z-scores of each function to percentage from the maximum (5% percentile of maximum values for each function to avoid outliers), and obtained the number of functions beyond a given threshold. We used thresholds from 5 to 100%, and obtained the distributions of the number of functions beyond these thresholds. Then we applied Gaussian mixture models to find the number of modes in the number of functions above the threshold (Figure S 5.4). The histograms of the number of functions above thresholds higher than 65% produced too few bins to perform a reliable Gaussian mixture analysis (almost all sites only had 0-3 functions higher than 65% respect to the maximum values), so this analysis was performed using thresholds from 5 to 65%. We assessed the bimodality by subtracting the BIC for unimodality and bimodality in a Gaussian mixture approach using Matlab. This metric, called ΔBIC , is positive if bimodality is achieved, and negative if the resulting simulated distribution is unimodal.

The results of these analyses confirmed that bimodality is consistent regardless of the method employed for assessing multifunctionality. They also show that bimodality is probably caused by several of the functions we measured

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(phenols, aromatic compounds and organic carbon, phosphatase activity, total nitrogen and total phosphorous). By using the threshold approach (Byrnes et al. 2014) we found that bimodality in ecosystem multifunctionality remains when measuring it as the number of functions exceeding multiple thresholds instead of the averaging index.

We also evaluated whether the two alternative states in multifunctionality found were caused by the particular subset of sites selected for this study. For doing so, we further analyzed multifunctionality values obtained for the entire dataset from Maestre et al. (Maestre et al. 2012a). Multifunctionality was also bimodal when using the 224 sites of this dataset instead of the 115 used here (BIC for one and two modes were 366.7 and 365.2 respectively; and AIC 359.8 and 348).

Although bimodality might be interpreted as the existence of two different alternative states, it may also be confounded by a bimodal distribution of the drivers of multifunctionality. This is unlikely, as the two multifunctionality states co-occurred across a range of aridity values (see Figure 5.4 in the manuscript). Nevertheless we conducted sensitivity analyses, based on Monte-Carlo randomizations, to control for this potential confounding factor. We performed a regression between multifunctionality and aridity, obtained the parameters describing this relationship and a distribution of the residuals from this regression. By using these parameters and the aridity data, and by adding random residuals generated from the residuals distribution obtained, we simulated 1000 theoretic sets of multifunctionality values derived from a linear combination of aridity (Figure S 5.1.). We assessed the bimodality of these generated values by using the Δ BIC metric (positive if bimodality is achieved). Our results show that most of the simulations were unimodal, meaning that the bimodality in ecosystem multifunctionality we found in our analyses is highly unlikely ($P = 3.6 \cdot 10^{-10}$) to have been driven by a confounding effect of the bimodal distribution of aridity in our data (Figure S 5.5.). The same simulations using AIC instead of BIC yielded very similar results ($P = 5.9 \cdot 10^{-13}$).

SUPPLEMENTARY FIGURES

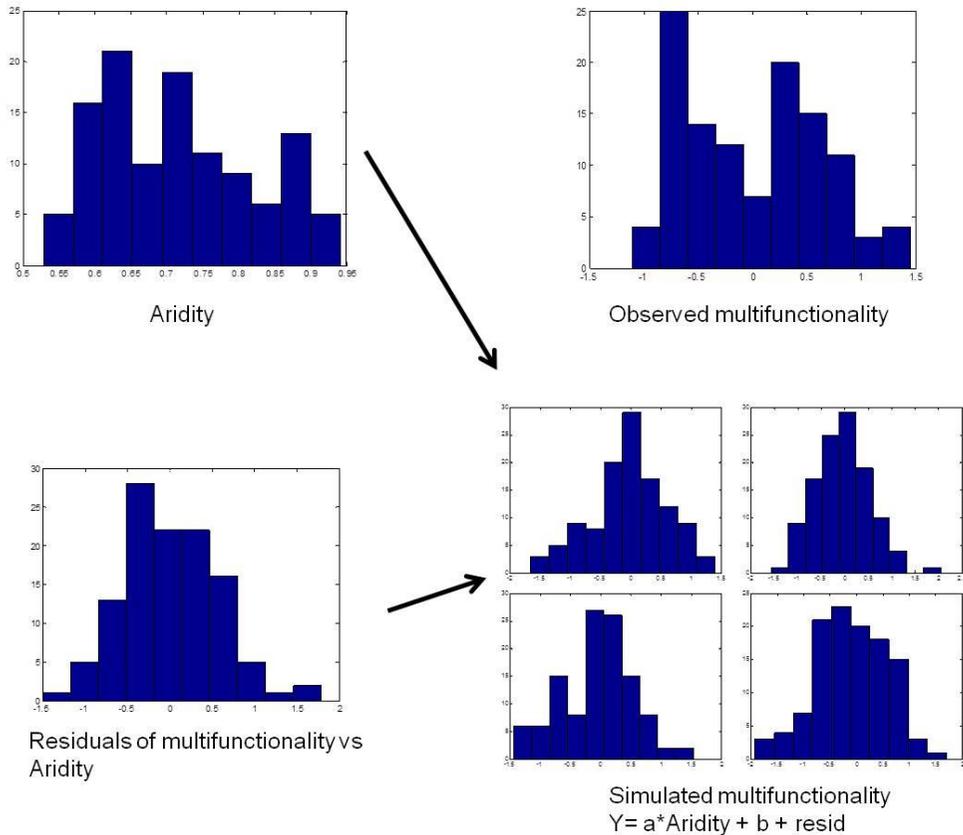


Figure S 5.1. Outline of monte carlo analysis performed to assess effects of the bimodal distribution of the aridity on that of multifunctionality.

Diagram showing the Monte-Carlo procedure used to generate simulated distributions of multifunctionality (displayed on bottom right) from linear combinations of aridity data (distribution displayed on top left) with the residuals obtained for multifunctionality after controlling for the effect of aridity (distribution displayed in bottom left). The observed distribution of multifunctionality in our 115 study sites is displayed on the top right panel.

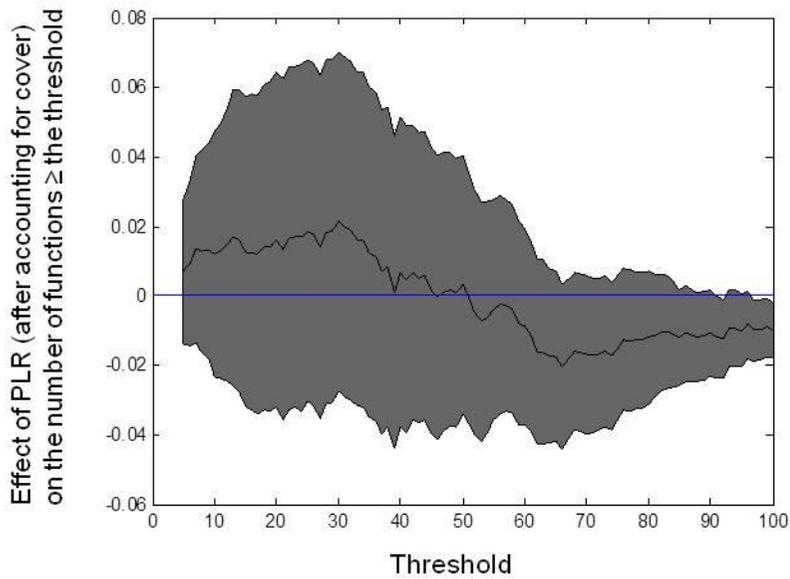


Figure S 5.2. Relationship between patch-size distributions and the number of functions above different thresholds.

Effect of power law relative range (PLR) on the residuals of the number of functions beyond different thresholds after accounting for the effects of plant cover (x-axis). The shaded area indicates the 95% confidence intervals of the slope. The blue line indicates the 0 slope line; if this line is within the shaded area no significant effect occurs.

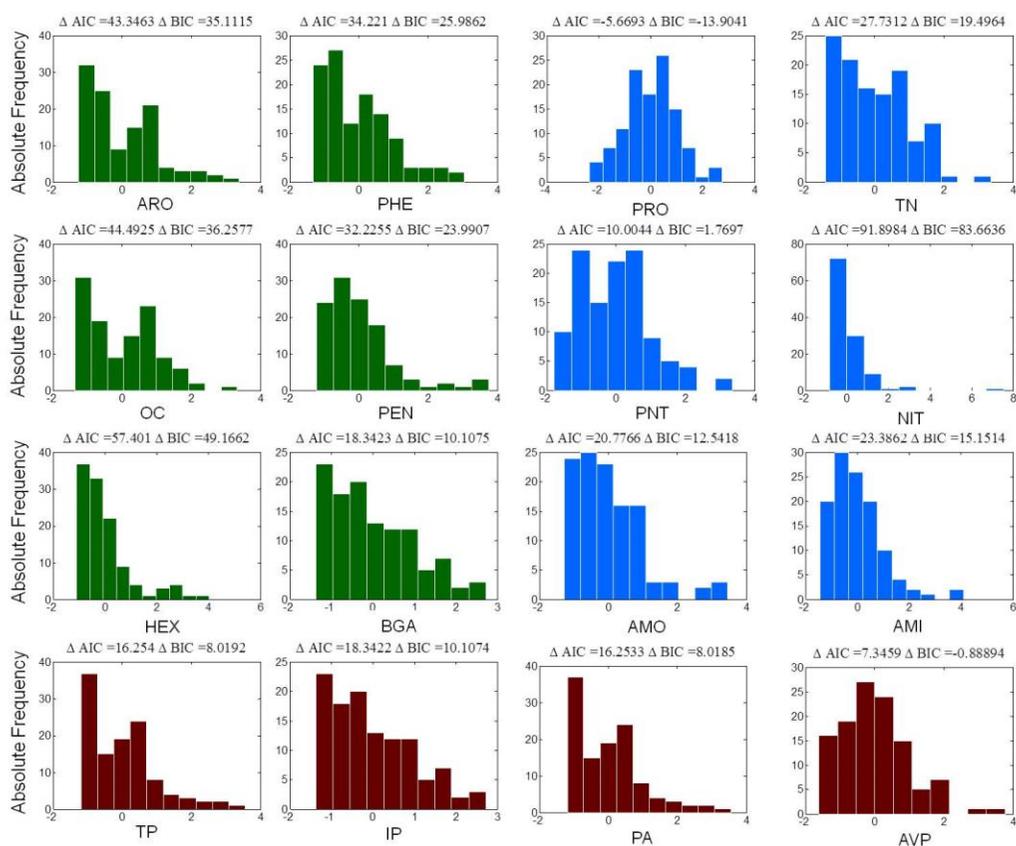


Figure S 5.3. Frequency distribution of all functions evaluated.

Functions from the carbon, nitrogen and phosphorus cycles are in green, red and blue, respectively. The difference in information criteria (IC; ΔAIC for Akaike information criterion and ΔBIC , for Bayesian information criterion) between unimodal and bimodal distributions are shown on top of each panel (in Gaussian mixture models: IC with one mode – IC with two modes; hence positive if bimodal since $IC_2 < IC_1$). PRO: proteins; AMI: amino acids; NIT: nitrates; TN: total nitrogen; OC: organic carbon; TP: total phosphorous; IP: inorganic phosphorous; PA: phosphatase activity; AVP: available phosphorous; BGA: beta-glucosidase activity; ARO: aromatic compounds; PNT: nitrogen transformation rate; PHE: phenols; HEX: hexoses; PEN: pentoses; AMO: ammonium.

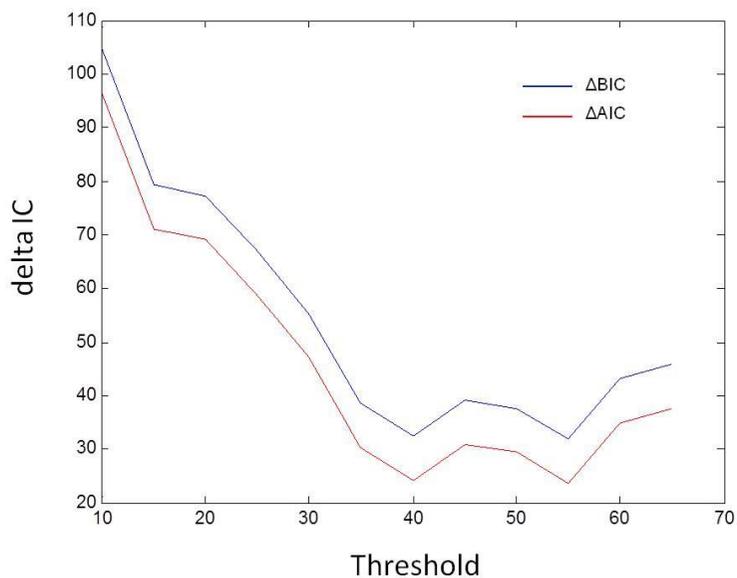


Figure S 5.4. Bimodality in the number of functions above different thresholds.

Differences of information criterions (ΔIC) obtained in a Gaussian mixture models analysis of the number of functions beyond a given threshold respect to their maximum. ΔIC is calculated as IC with one mode – IC with two modes; hence positive if bimodal since $IC_2 < IC_1$.

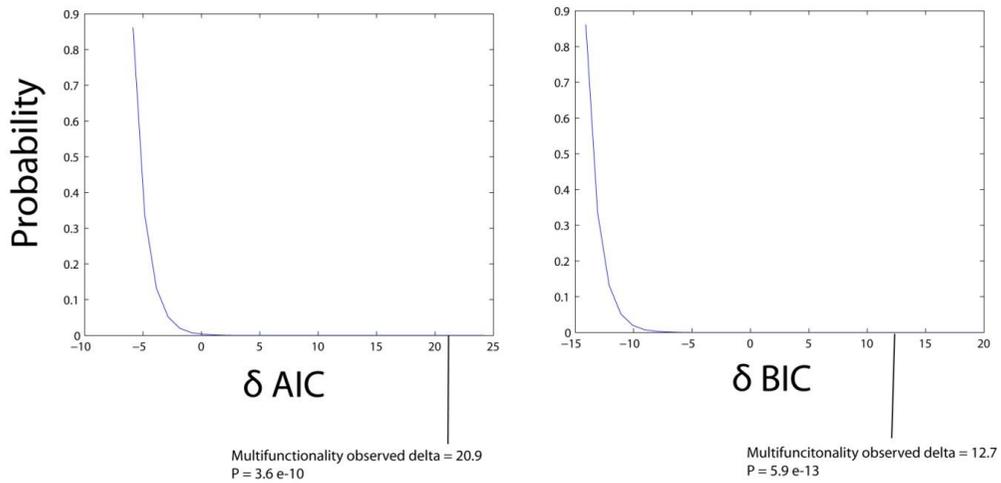


Figure S 5.5. Probability of finding bimodal patterns of multifunctionality because of aridity.

Probability density functions obtained with the Monte Carlo simulations explained in Fig. S 5.1 of different Δ AIC (A) and Δ BIC (B) values. Positive and negative values of Δ AIC and Δ BIC mean bimodal and unimodal distributions, respectively. The values obtained when analyzing the multifunctionality data observed in our study sites are pointed by arrows.

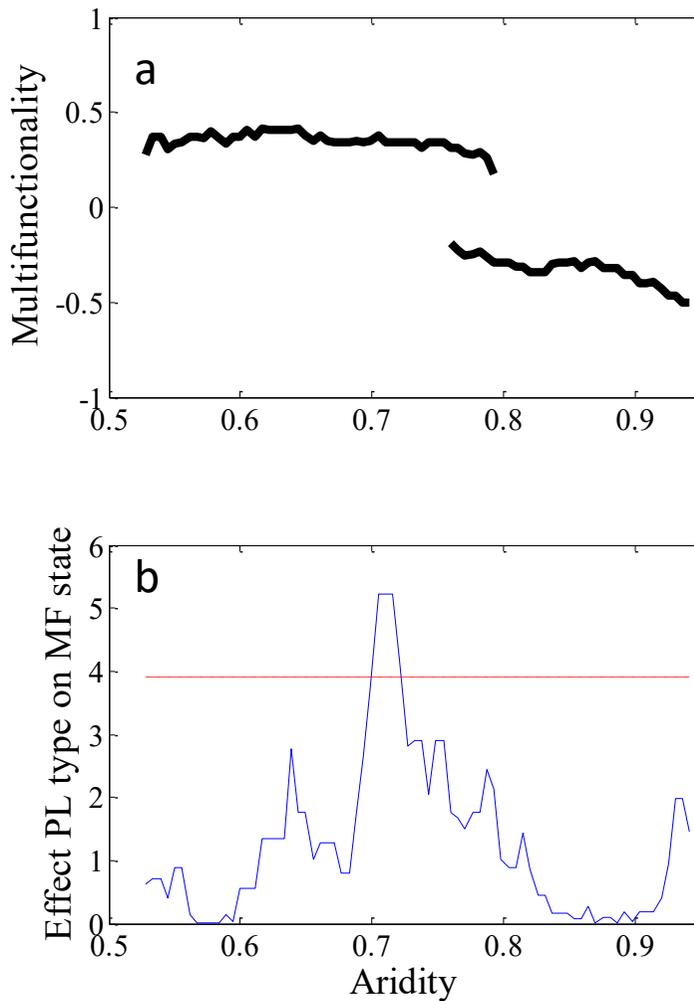


Figure S 5.6. Association between changes in patch size distributions and multifunctionality across an aridity gradient.

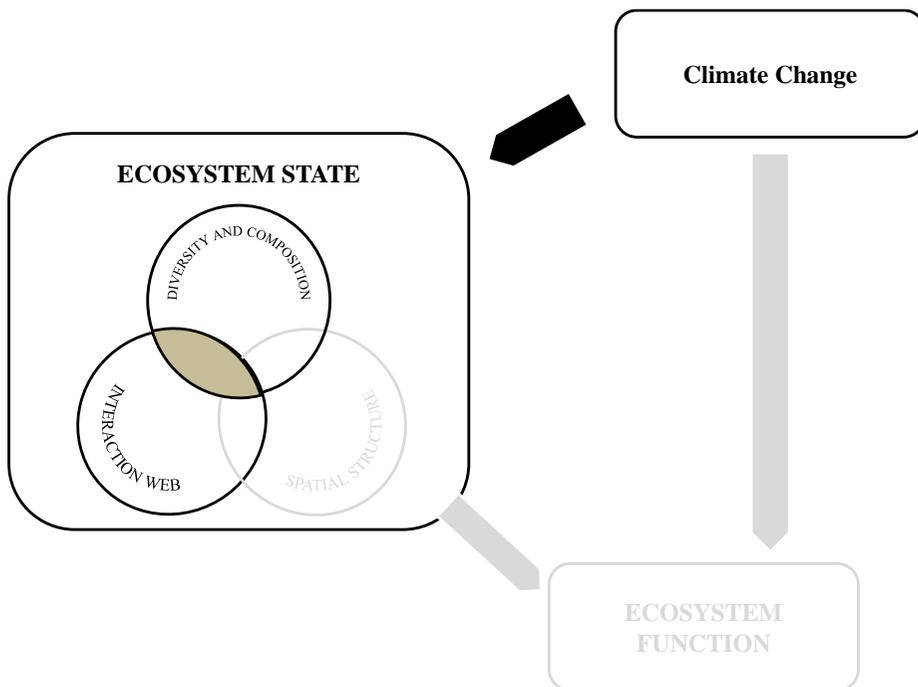
a) Multifunctionality alternative states throughout the aridity gradient studied (computed as local minima of estimated potential energy as in Figure 5.4). b) Association between patch size distribution type (PL/non PL-like) and multifunctionality (High /Low) throughout a moving window in aridity. Association is calculated as the Chi-Square metric between both variables. Red dashed line indicate threshold for $P < 0.05$.

Table S 5.1. Linear relationship between patch-size distributions, plant cover and ecosystem functions.

Correlation coefficients of the relationships between different functions and power law relative range (PLR), plant cover (TCT) and PLR when accounting by TCT with partial correlations (PLR|TCT). *P* values are shown between brackets and highlighted in bold if below 0.05. PRO: Proteins; AMI: amino acids; NIT: Nitrates; TN: Total Nitrogen; OC: organic carbon; M: multifunctionality; TP: total phosphorous; IP: inorganic phosphorous; PA: phosphatase activity; AVP: available phosphorous; BGA: beta-glucosidase activity; ARO: aromatic compounds; PNT: nitrogen transformation rate; PHE: phenols; HEX: hexoses; PEN: pentoses; AMO: ammonium; M: multifunctionality

		PLR	TCT	PLR TCT
NITROGEN CYCLE	NIT	-0.03 (0.780)	0.21 (0.022)	-0.16 (0.080)
	AMO	0.12 (0.201)	0.39 (0.001)	-0.1 (0.267)
	TN	0.3 (0.001)	0.48 (0.001)	0.07 (0.450)
	PNT	0.2 (0.031)	0.33 (0.001)	0.04 (0.682)
	AMI	0.11 (0.230)	0.3 (0.001)	-0.05 (0.585)
	PRO	0.11 (0.236)	0.24 (0.011)	-0.01 (0.877)
CARBON CYCLE	OC	0.34 (0.001)	0.54 (0.001)	0.08 (0.372)
	PEN	0.29 (0.001)	0.28 (0.002)	0.18 (0.058)
	HEX	0.13 (0.153)	0.35 (0.001)	-0.06 (0.525)
	ARO	0.24 (0.010)	0.27 (0.003)	0.12 (0.201)
	PHE	0.17 (0.064)	0.31 (0.001)	0.02 (0.871)
	BGA	0.23 (0.014)	0.38 (0.001)	0.04 (0.658)
PHOSPHOROUS CYCLE	AVP	-0.19 (0.039)	-0.08 (0.396)	-0.18 (0.059)
	PA	0.14 (0.125)	0.44 (0.001)	-0.11 (0.254)
	IP	0.23 (0.014)	0.38 (0.001)	0.04 (0.658)
	TP	0.14 (0.125)	0.44 (0.001)	-0.11 (0.254)
M		0.26 (0.006)	0.53 (0.001)	-0.02 (0.8)

Species-specific adaptations determine how aridity and biotic interactions drive the assembly of dryland plant communities



Miguel Berdugo, Fernando T. Maestre, Sonia Kéfi, Nicolas Gross, Yoann Le Bagousse-Pinguet, Santiago Soliveres

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ABSTRACT

We disentangled individual and interacting effects of plant-plant interactions, abiotic factors and species-specific adaptations as drivers of community assembly, a question at the core of ecology hampered by the challenges to separate abiotic/biotic factors. Merging species distribution models and local spatial patterns, we isolated the relative importance of these abiotic/biotic factors in the assembly of dryland plant communities. Facilitation benefitted generalist species and those maladapted to local environmental conditions and, with aridity, was the strongest assembly driver globally. Competition, instead, affected species abundances in communities dominated by specialist species and under the most arid conditions. Due to community specialization, the importance of aridity in shaping dryland plant communities peaked at moderate, not high aridity levels. We show that species-specific adaptations determine how aridity and plant-plant interactions drive local species abundances, helping to better understand the consequences of ongoing climate change on community assembly in drylands, the largest biome on Earth.

Keywords: Community assembly, species-specific adaptation, facilitation, competition, niches

INTRODUCTION

Climate change is affecting biodiversity by reducing local species richness, altering composition and homogenizing biotas in terrestrial ecosystems worldwide (Millennium Ecosystem Assessment 2005). To better understand how these changes will impact ecosystem structure and functioning, it is important to accurately predict future community composition and local species abundance (Chapin III et al. 2000, Valencia et al. 2015). Approaches to forecast future species occurrences at global, continental or regional scales typically use species distributions models (SDMs hereafter; (Guisan and Thuiller 2005). These models rely on abiotic variables, such as climate and soil type, and are able to predict diversity changes and extinction risks at regional scales (e.g., Araújo *et al.* 2002). However, scaling down these models at the community level is challenging because of biotic interactions and dispersal limitation, which largely influence local species abundance (Weiher and Keddy 2001).

Disentangling how abiotic variables and biotic interactions assemble communities is a difficult task because both processes usually interact and mask each other (Lawton 1999, Mayfield and Levine 2010). As a result, our understanding of how these abiotic and biotic assembly drivers determine local plant species abundance is limited and does not allow performing reliable predictions on the response of plant communities to ongoing climate change. Combining approaches focusing on contrasting spatial scales, such as species distribution models (SDMs, applied at regional scales) and local spatial segregation and aggregation data (applied at local scales) can help to tease apart the relative importance of abiotic and biotic assembly drivers (Figure 6.1). SDMs provide a good modelling framework to account for the effect of large scale abiotic factors, and therefore can help to identify the upper limit of species abundance within a community based on its environmental suitability for the different species in the pool (VanDerWal et al. 2009). Spatial co-occurrence patterns observed within communities can inform about the frequency and strength of plant-plant interactions (e.g., Cavieres *et al.* 2006), but provide limited information about the role of abiotic factors. Along with their ability to describe environmental suitability of individual species, SDMs allow to assess species adaptive strategies such as the degree of specialization to environmental conditions (Devictor et al. 2010), an important parameter to predict the outcomes of biotic interactions (Liancourt et al.

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2005, Gross et al. 2010). For instance, species specialized to local environmental conditions are less likely to be facilitated and do not need nurses to thrive (Liancourt et al. 2005). Specialized species are also more likely to compete against each other (Greiner La Peyre et al. 2001). Thus, species-specific differences in the degree of specialization to the local environment may strongly influence the importance of plant-plant interactions in explaining local species abundances. Despite SDMs and local co-occurrence patterns hold complementary information about the importance of abiotic/biotic assembly drivers, they are often used separately.

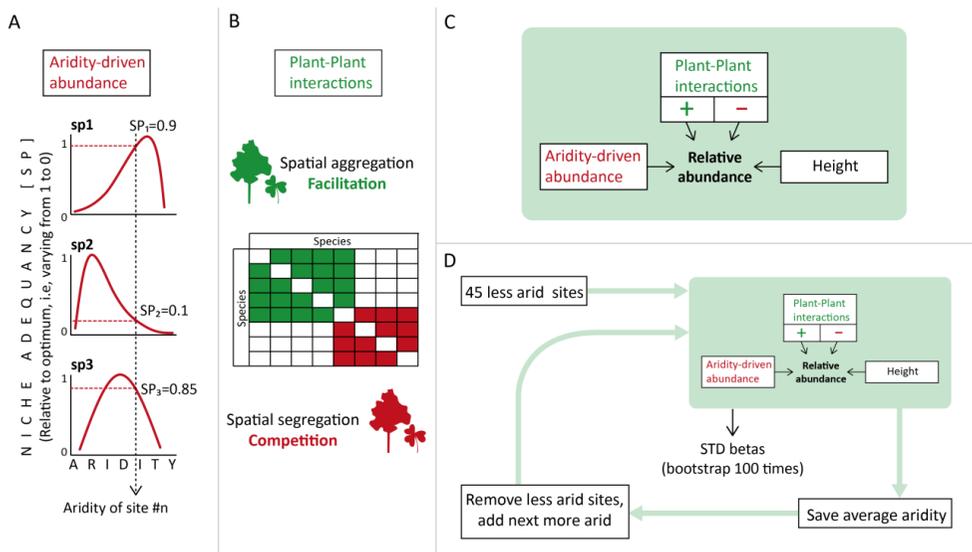


Figure 6.1. Methodological approach followed.

First, we obtained, for each species, the Aridity-driven abundance using species distribution modelling with aridity as predictor (a) and spatial co-occurrences measured in the field (as a proxy of plant-plant interactions, b). Then we built the model by additionally controlling for species size and using the relative abundance of species as response variable (c). The effects of these elements on species abundance is a metric on the importance of each assembly driver evaluated (aridity, facilitation and competition) for community assembly. Finally, we used a moving window approach to explore how the importance the different community assembly drivers change along aridity and community specialization gradients (d). SP: Species Performance, STD: Standardized coefficients.

Here we combine, for the first time, SDMs with local co-occurrence data to test the relative importance of abiotic factors, plant-plant interactions and the degree of specialization, as well as their interplay, as drivers of species abundances

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within communities. We used data gathered from 157 drylands from all continents except Antarctica. These ecosystems are constrained by water scarcity (Whitford 2002), and the interplay of aridity with plant-plant interactions (competition and facilitation) largely drives the composition and diversity of their plant communities (Tielbörger and Kadmon 2000, Tirado and Pugnaire 2003, Soliveres and Maestre 2014). Drylands already cover over 45% of terrestrial surface and forecasted increases in aridity will expand their global extent by 11-23% by the end of this century (Průvka 2016). Hence, understanding how the relative importance of abiotic/biotic assembly drivers changes along aridity gradients is crucial to predict the response of terrestrial ecosystems to ongoing climate change. Specifically, we hypothesized that: i) species become more adapted and specialized to aridity as the latter increases, ii) aridity and plant-plant interactions (both facilitation and competition) interact to drive community assembly, and iii) in communities dominated by species specialized to aridity, facilitation is less important than competition as an assembly driver.

MATERIALS AND METHODS

Study sites and field sampling

The 157 sites used in this study are a subset of the 236 sites used of Ulrich *et al.* (2016), and were located in drylands from 19 countries (Figure S 6.1). The sites surveyed differ widely in their environmental conditions: annual mean temperature, rainfall and elevation ranges are from -1.8 to 27.8 °C, from 67 to 1219 mm, and from 69 to 4668 m.a.s.l., respectively. Our database includes grasslands, shrublands and savannahs, with species richness ranging from 2 to 52 perennial species, and total plant cover ranging from 2 to 82 %.

All the sites were surveyed between 2006 and 2013 according to a standardized sampling protocol (see Maestre *et al.* 2012 for details). In each of these sites, a 30 m x 30 m plot was established and four 30-m long transects were displayed separated by 8 m from each other. We established 20 quadrats (1.5x1.5m) along each transect (80 per site) and visually estimated the cover of each perennial plant species, which was used as our surrogate of species abundance in each quadrat. A total of 898 species were identified to the species level. We

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calculated the aridity level of each site [$1 - \text{aridity index (AI)}$, where AI is the precipitation/potential evapotranspiration] from AI obtained from the Global Potential Evapotranspiration database (Zomer et al. 2008), which is based on interpolations provided by WorldClim (Hijmans et al. 2005).

We developed a four-step approach to evaluate how abiotic and biotic factors determine species relative abundance in plant communities. First, we extracted the aridity niches of all species surveyed using SDMs, and extracted the local relative abundance of species expected when considering only abiotic conditions. Then, we estimated the main features of species niche (niche optimum, niche breadth and niche skewness), calculated a community-weighted mean of such features, and evaluated their variation along aridity gradients to identify changes in common strategies of species specialization to aridity across environmental gradients. Third, we evaluated the effect of both aridity and plant-plant interactions (as extracted from co-occurrence analyses) on the relative abundance of species within each community. Finally, we evaluated changes in the relative importance of abiotic/biotic assembly drivers along gradients of aridity and of niche specialisation of the species in our communities. These steps are described in detail below.

Step i - Assessing aridity niches using species distribution models

SDMs are nonlinear statistical models relating abiotic variables (predictors) with species occurrences (response variable) at regional or global scales. We obtained species occurrences from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>). For simplicity, we used only aridity as the sole abiotic factor for our SDMs. Aridity is a good proxy for water availability, which is the most influential abiotic factor for plant survival in drylands (Whitford 2002), and is a key determinant of both species interactions and composition in drylands (Callaway 2007, Soliveres and Maestre 2014).

We performed SDMs using MAXENT (Elith *et al.* 2011) as fully described in Appendix 3.1. The result of MAXENT is a function relating the suitability of a species with aridity (i.e., the “aridity niche”). Based on the aridity niches, we then estimated the “aridity-driven abundance” (Aab), i.e., the expected local relative abundance of each species based solely on the aridity level of each surveyed site and the other species able to colonize the site (see Figure 6.1.a).

$$Aab_i = \frac{SP_i}{\sum_{j=1}^{nsp} SP_j}$$

equation 6.1

where nsp is the number of species in the community, SP is the species performance calculated as the habitat suitability for the species yielded as an interpolation between the species niche and the aridity observed in the surveyed communities. To ensure comparability of SP , we standardized niches to their maximum (thus it ranged between 0 and 1 for each species). This methodology assumes that, for a particular environmental condition, a species will share the available space with its neighbors by occurring proportionally to its aridity preferences (as measured with the aridity niches). We assumed that relative abundances in the community emerge from sampling the species pool according to the local aridity level, thus, the relative abundance is the density expectation of sampling all species present in the community, each with a probability that depends on its SP .

Step ii – Identifying dominant plant strategies based on niche features

Aridity niches hold information about the adaptive strategy of species by showing the following features: i) niche optimum (the aridity level at which a species performs optimally, $SP = 1$), ii) niche breath (the aridity range that a given species occupies), and iii) niche shape (as measured by the skewness of aridity niches; see examples in Figure S 6.2). As this information is available for each species, each niche feature can be considered as an attribute of the species related to its response to aridity. These attributes can be used to scale species response to aridity at the community level, i.e. to track how the dominant plant strategy and their diversity within communities change across the global aridity gradient.

First, we calculated the community weighted mean niche optimum obtained as the sum of species niche optimum weighted by their observed relative abundance (adapted from Lavorel & Garnier 2002, hereafter CW-niche optimum) as a measure of the tolerance of communities to aridity. CW-niche optimum was used to evaluate how well the optimum level of aridity of a given species matched with the observed aridity in the surveyed sites. Differences between CW-niche optimum and observed aridity may impact the importance of aridity-driven abundance as a community assembly driver, as it supposes extra stress to species

maladapted to local conditions. We used this analysis to understand variations in the importance of aridity-driven abundance (see step iv) across aridity gradients. Additionally, this analysis indicated whether information extracted from SDM matched the one provided by observed patterns, as the local abundance of a species in a given community should exhibit aridity optima around the local aridity conditions of such community (meaning that the community is locally adapted to the aridity).

Second, we calculated the community weighted mean of niche breadth (CW-Niche breadth) and shape (CW-Niche skewness) to assess the degree of species specialization to aridity. A smaller niche breadth defines species specialized to a particular range of aridity conditions, whereas the shape informs about the preference of such species for more or less arid environments. Hence, communities dominated by species specialized to aridity will be defined by lower CW-Niche breadth and negative CW-Niche skewness (i.e., right-skewed, indicating preferences for high aridity level). We observed a strong correlation between niche breadth and skewness ($r > 0.60$): communities dominated by species with a narrow niche breadth tend also to be dominated by species with a negative skewness (Fig. 2). Therefore, we used only CW-Niche skewness as a measure of the community specialization towards arid environments (community specialization) in further analyses.

Step iii – Developing a statistical model to predict species abundance

Plant-Plant interactions: Expected abundance using co-occurrence matrices

For each site, we obtained an estimate of the expected relative abundance of each species according only to plant-plant interactions, measured as spatial co-occurrences. We used aggregation/seggregation as proxies of facilitation/competition, respectively (Tirado and Pugnaire 2003, Cavieres et al. 2006, Valiente-Banuet and Verdú 2008). We are aware that spatial aggregation/seggregation can also be driven by other factors such as habitat sharing or seed capture (Morales-Castilla et al. 2015). Interpretation of the results should then consider this limitation; however, co-occurrence has been successfully linked to plant-plant interactions as estimated from manipulative studies (Tirado and Pugnaire 2003), and is the only method available to approximate facilitation and competition at the community level when studying many sites and species (Cavieres et al. 2006, Valiente-Banuet and Verdú 2008).

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As a metric of spatial aggregation/segregation, we obtained a normalized score of co-occurrence using PAIRS (Ulrich 2008). PAIRS randomizes the matrices of species occurrences within the quadrats (one per site) and detects deviations from random spatial association patterns in all species pairs while controlling for false positives due to multiple testing (Gotelli and Ulrich 2010). We used an abundance-weighted swap method to randomize species occurrence. This method assumes sampling quadrats with equal probabilities of being colonized and keeps species richness and local abundances constant to account for overall differences in habitat suitability. We obtained co-occurrence in both observed vs. randomized communities for each species pair in each community as:

$$Co - occurrence_{ij} = (n_i - N_{ij})(n_j - N_{ij}) \quad \text{equation 6.2}$$

where n is the number of occurrences of target species (n_i) and its neighbours (n_j), and N is the number of co-occurrences of both species together. We used the standardized effect sizes obtained from comparing co-occurrences of the null model with that observed in the field as a metric of the strength of the interaction between target species and their neighbours as a function of the deviation from random co-occurrence of species i and j . Thus, standardized effect sizes are comparable between different pairs, but do not take into account how frequent the interaction is within the community. To correct for this, we estimated the relative abundance of a species i expected due to competition (i.e., negative co-occurrence, equation 3) and facilitation (i.e., positive co-occurrence, equation 4) with other species (j , not including i) as:

$$Cab_i = \sum_{j=1}^{nsp} |\beta_{j \rightarrow i}| * p_j \quad \text{iff } \beta_{j \rightarrow i} < 0 \quad \text{equation 6.3}$$

$$Fab_i = \sum_{j=1}^{nsp} \beta_{j \rightarrow i} * p_j \quad \text{iff } \beta_{j \rightarrow i} > 0 \quad \text{equation 6.4}$$

Where, Cab and Fab represents the competition and facilitation-driven abundances in the community; β represents the standardized effect sizes obtained measuring the competitive (if negative) and facilitative (if positive) effects over species i of other species in the community (j), and p_j represents the relative abundance of species j in the surveyed community. By doing this we obtained a

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metric of the effects of plant-plant interactions on the performance of target species for a specific community considering both the strength of interaction with each neighbor (standardized effect sizes) and the frequency of such interactions within the community (relative abundance of the neighbours).

Fitting the statistical model

We used linear mixed models to model the relative abundances of each surveyed species as a function of: i) aridity-driven abundance, ii) cumulative effects of both competition-driven and facilitation-driven abundances, and iii) the height of the target species (equation 5, Figure 6.1.c). Plant height was introduced to control for potential confounding effects between cover (used to estimate relative abundance in the field) and the size of the species being sampled (taller species are more likely to score higher cover values regardless of their abundance). Plant height was obtained from available databases, published literature and local floras (see Appendix A from Soliveres *et al.* 2014 for a full reference list). Species-specific differences were accounted for by introducing “species identity” as a random factor in the model to avoid the use of the same species in two different communities as two independent cases.

As species relative adaptation to local aridity may influence the importance of facilitation and competition (Liancourt *et al.* 2005, Gross *et al.* 2010, Soliveres *et al.* 2014a), we established an interaction between aridity-driven (derived from the niches and summarizing species suitability to local conditions) and competition- and facilitation-driven abundances. Interactions between aridity and competition and facilitation will be positive if the effect of plant-plant interactions on relative abundance is higher for locally adapted species than for species not adapted to local conditions. It must be noted that the effects of competition are negative, therefore positive contributions from the interaction term decrease the effect of competition on the relative abundance of species adapted to local aridity conditions. Thus, our final model was:

$$AbRel_i = AAb_i * FAb_i + AAb_i * CAb_i + size_i + (1|sp_i) \text{ equation 6.5}$$

Where *AAb*, *FAb* and *CAb* represent aridity, facilitation and competition-driven abundances, respectively. *Size* is the height of species *i*. We obtained the

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standardized effect sizes of all variables on relative abundance. We assume that the effect size of how suitable the local aridity is for a given species (AAb) and plant-plant interactions on relative abundance represent the relative importance of abiotic factors and plant-plant interactions, respectively, as drivers of the assembly of the communities analyzed.

Step iv –Exploring changes in the relative importance of biotic/abiotic assembly drivers across gradients of aridity and community specialization

First, we ordered all sites according to either aridity or community specialization (contingent factors). Then, we took the 45 sites with the lowest values of each contingent factor (as this number of sites allowed sufficient statistical power for our model), and performed the mixed model described in equation 5 (see Figure 6.1.d). In the case of community specialization, we did not use the interaction terms described in equation 5. We did so because CW-Niche skewness already summarizes the influence of species adaptation on the importance of plant-plant interactions and, therefore, the information extracted from interaction terms is redundant with that extracted from the gradient.

We bootstrapped the standardized slopes of each predictor to obtain their confidence intervals, which were matched to the average value of the contingent factor studied across the 45 sites. Next, we removed the community with the lowest value of the contingent factor studied from the 45 selected sites, and added the community scoring the next higher value to repeat the same calculations. We repeated this loop as many times as sites remained (112). The coefficients of the standardized predictors included in the linear mixed models provide a comparable measure of the importance of plant-plant interactions and position of each species regarding its aridity niche. We used the 95% confidence interval to assess changes in the importance of biotic/abiotic assembly drivers across the gradients studied.

Further statistical details

To maintain information representative of the community level in the analyses described in steps ii, iii and iv above, we used all sites for which we gathered enough information (e.g., discarding species with less than 20 occurrences [see appendix 3.1], or those for which we could not retrieve height values) for the species that summed up at least 60% of the total perennial vegetation. A total of

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157 out of the original 236 communities remained for further analyses, leaving a total of 1631 study cases (405 different species in 157 communities with some species repeated throughout communities). The species from these communities represented on average of 91.6 ± 10.3 % (mean \pm SD) of the total cover in the surveyed sites.

Mixed models in steps ii and iv were performed using the “lme4” R package (Bates et al. 2015) in R (R Development Core Team 2008). We log transformed all variables but aggregation and segregation (which were double square root transformed), and scaled the values after transformation to fulfill the assumptions of the analyses and to obtain standardized coefficients. We extracted the marginal (variance explained by fixed factors) and conditional (variance explained by fixed + random factors) R^2 values (Nakagawa and Schielzeth 2013) using the “piecewiseSEM” R package (Lefcheck 2015).

In analyses of steps ii, and iv we used generalized additive models (Wood 2006) to depict smoothed trends in the effects of community niche features and assembly drivers across gradients of aridity and community specialization. These models are used to investigate the nonlinear character of these trends and work well when a large number of replicates is considered (Wood 2006). Data and code used to perform all the analyses are available in figshare (Berdugo et al. 2017b).

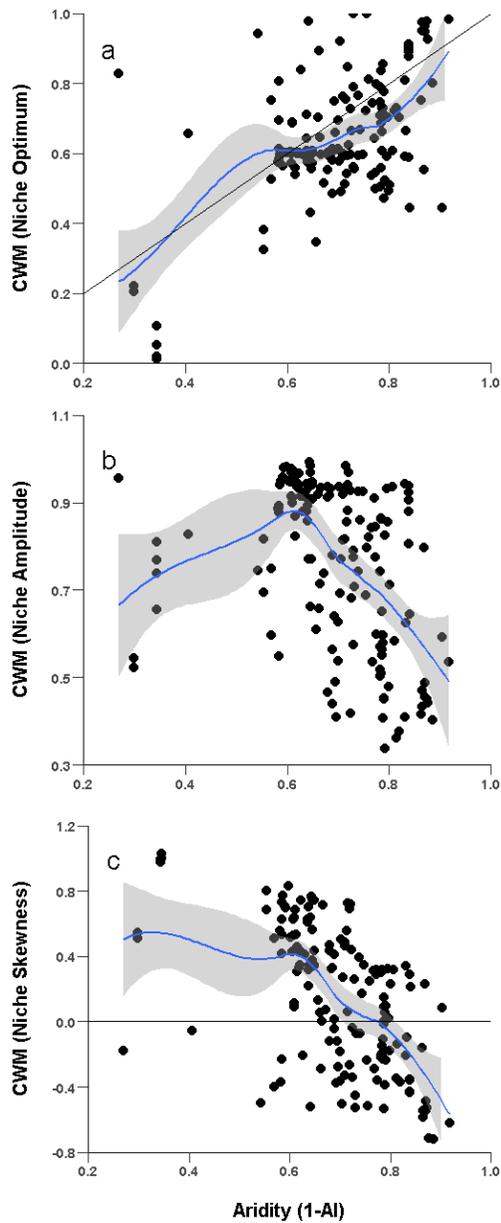


Figure 6.2. Trends of niche features with aridity.

Relationships between aridity and the community weighted mean (CWM) of the niche optimum (a), niche breadth (b) and niche skewness (c) obtained from species distributions models. The blue line and shaded area are the gam-smoothed trends (non-parametric regressions) observed \pm 95% confidence interval, respectively. The black line in a) represents the 1:1 line; the 0 value in c) indicates a change in the direction of skewness.

RESULTS

Common strategies on species adaptive response along aridity gradients

The relationship between the CWM of aridity optima and observed aridity was close to the 1:1 line (slope = 0.8 ± 0.19), but deviated from this line at intermediate aridity levels (about 0.6-0.8; Figure 6.2a). Both CW-Niche skewness and CW-Niche breadth decreased within this aridity range, suggesting that species became more specialized to arid conditions by skewing their niches to the right (i.e., showing preference for more arid environments; Figures 6.2b and 6.2c). All these trends were not confounded by the uneven distribution of the number of communities across the aridity gradient (Figure S 6.3).

Changes in the relative importance of aridity and plant-plant interactions as assembly drivers

The strongest predictors of the relative abundance of each species were facilitation (measured as positive co-occurrences) and aridity, which exhibited similar effect sizes (Figure 6.3). Competition (negative co-occurrences) and the interactions between aridity-driven abundance and plant co-occurrences showed negative effects in the overall model. The negative effects of interaction terms suggest that adapted species in drylands usually experience less facilitative effects and more competitive effects.

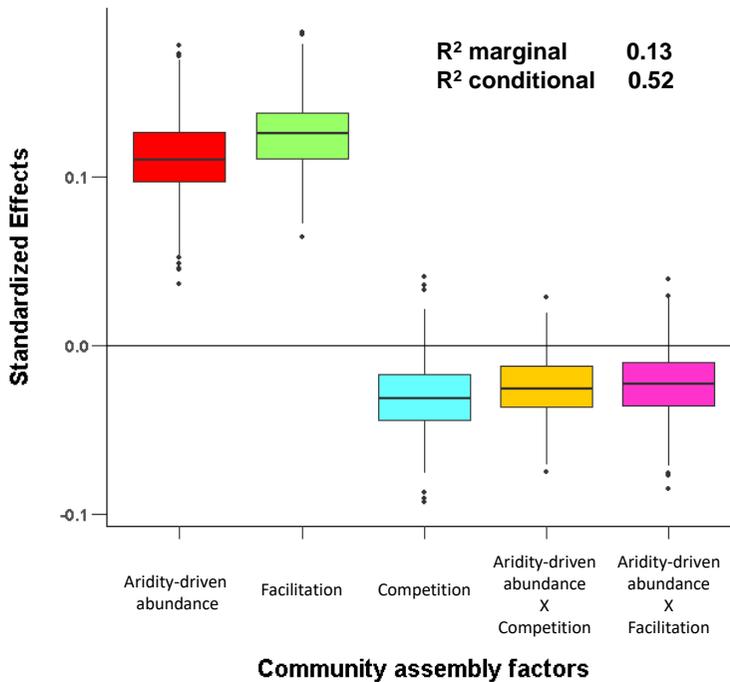


Figure 6.3. Assembly drivers global importance.

Standardized effect sizes of different drivers of community assembly obtained from the linear mixed model applied to all dryland communities. Median, 50 and 75 quantiles are represented in a box plot for each effect. Marginal (variance explained by fixed factors) and conditional (variance explained by fixed + random factors) R² values are shown.

The importance of aridity as an assembly driver increased up to aridity levels ~ 0.7 ; remaining constant beyond that value (Figure 6.4a, see also Table S 6.1). The effect of facilitation declined linearly, while that of competition increased (i.e., became more negative), with aridity. However, the effect of competition was only significant under very high aridity levels (0.75-0.80). The interaction term between aridity-driven abundance and competition shifted from negative at wetter sites to positive at dryer sites. These results indicate that, in the less arid sites of our gradient, competition was less important for species more adapted to local aridity than for those less adapted to them. Conversely, at high aridity levels, the effects of competition were stronger for species well adapted to aridity than for those that were far from their aridity optimum. The interaction term between response to aridity and facilitation turned negative (Table S1, Figure 6.4b), although only

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significant in some points of the gradient, with increasing aridity. This result suggests that, under high aridity conditions, facilitation tend to be a more important driver of species' abundances for those species maladapted to the observed (high arid) conditions.

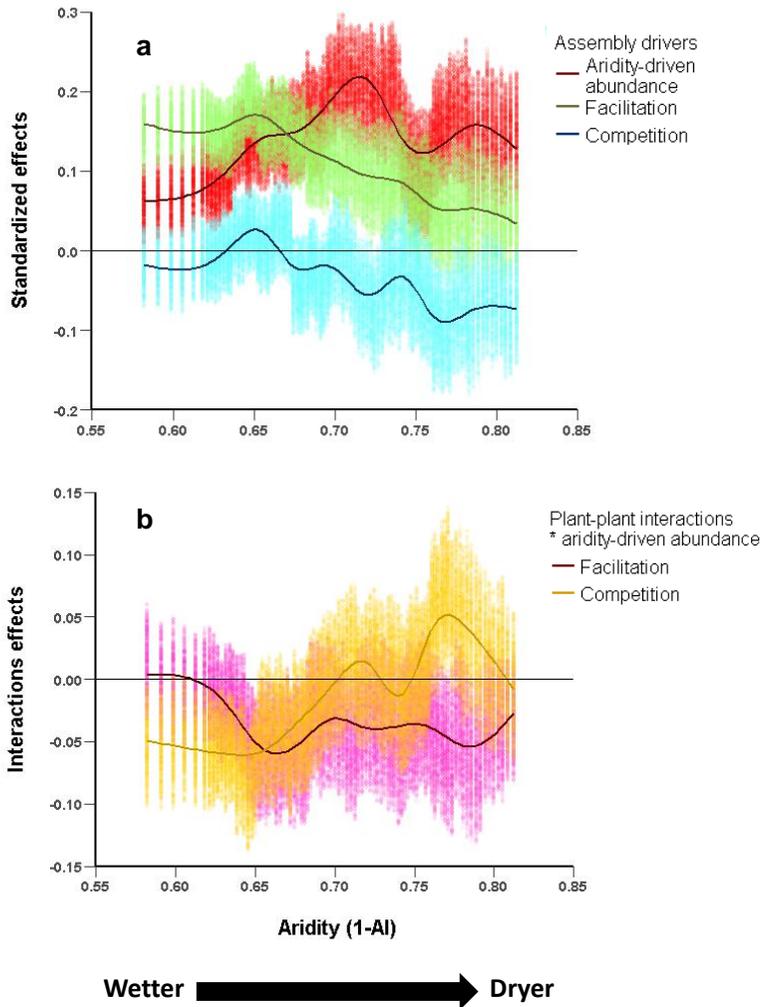


Figure 6.4. Importance of assembly drivers through aridity gradients.

Standardized effects sizes of facilitation, competition and local performance to aridity along an aridity gradient (a), and interactions between local performance to aridity and competition or facilitation (b). This analysis is performed by fitting a generalized mixed model throughout a moving window subsetting our study sites following the gradient of aridity. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects.

As communities became more specialized, the importance of facilitation as a community assembly process decreased (Figure 6.5). This corresponded with an increase of the importance of competition and aridity-driven abundance. The decline in the importance of facilitation was abrupt and became not significant around values of skewness=0, thus representing Gaussian-like shapes. These results remained consistent when using autoregression analyses instead of generalized additive models (Table S1).

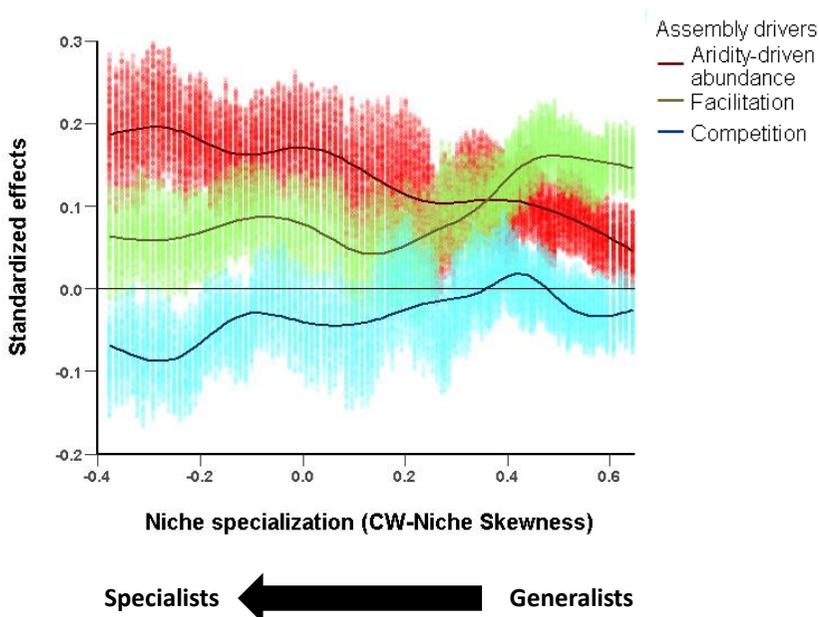


Figure 6.5. Importance of assembly drivers through specialization gradient.

Standardized effects sizes of facilitation, competition and aridity along a gradient of community specialization (measured as community weighted [CW] niche skewness). This analysis is performed by fitting a generalized mixed model throughout a moving window subsetting our study sites following the gradient of community specialization. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects.

DISCUSSION

Understanding what drives community assembly is a core ecological question that has proven particularly challenging. Here we used a new approach merging techniques at contrasting spatial scales to effectively tease apart abiotic/biotic drivers of species relative abundance. We found that facilitation (measured as positive spatial co-occurrences) and aridity largely explained community assembly of global drylands. The weak effects of competition and the interactions between abiotic and biotic drivers observed were explained by shifts in the importance of abiotic/biotic assembly drivers across gradients of aridity and specialization. We also observed a shift towards communities more specialized with aridity, which substantially reduced the importance of facilitation in the assembly of these communities. By showing the differential effect of abiotic conditions and plant-plant interactions according to current aridity levels and the degree of habitat specialization of the species pool to aridity, our study provides fundamental information on how species assemble in global drylands and may help to forecast future community composition in response to climate change.

Changes in abiotic/biotic controls of community assembly across aridity and specialization gradients

Our SDMs indicated that species niches became narrower and more skewed to dry conditions at aridity levels > 0.7 (Figure 6.2). This suggests a high degree of specialization of those species growing under more arid conditions, probably as an adaptive response of communities to increasing environmental harshness (Noy-Meir 1973, Devictor et al. 2010). In contrast to previous predictions that did not account for the degree of specialization of the species pool (Butterfield 2015), our results also suggest that communities already experiencing high levels of aridity should not be expected to drastically shift their composition with further aridification. The latter is supported by the asymptotic trend on the importance of aridity-driven abundance in the most arid drylands (Figure 6.4a for aridity > 0.75 , Figure 6.5), and the lower levels of beta-diversity found in these communities (Ulrich et al. 2014). Our results highlight the importance of including the degree of specialization of the species pool to accurately forecast compositional shifts with climate change, as highlighted by Bush *et al.* (2016).

Concomitantly, specialization of the species pool affected also the relative importance of plant-plant interactions at the community level (Figure 6.5, Figure S 6.5). Our findings suggest that the assembly of communities dominated by specialist species are less dependent on facilitation and more on competition, as it has been suggested also by other experimental studies (e.g., Liancourt *et al.* 2005; Gross *et al.* 2010). Our results, therefore, validate the occurrence of a tight relationship between species specialization and the outcomes of plant-plant interactions within plant communities. As specialists became dominant in high aridity sites (Figure 6.2b and c), the community-scale importance of facilitation declined, and that of competition increased, along the aridity gradient evaluated (Figure 6.4a). However, within high aridity sites, facilitation was still more important for species not adapted to local aridity conditions than for those not adapted to them (Figure 6.4b). Overall, our results support the notion that facilitation is less important for locally-adapted species, and that plant-plant interactions depend more on species-specific adaptations than on the overall environmental harshness (Liancourt *et al.* 2005, Soliveres and Maestre 2014).

By using a method that is more sensitive to the abundance patterns of interacting species rather than to species richness, we found a shift on the relative importance of facilitation and competition around aridity levels of 0.75-0.80. This suggests a collapse of facilitation as a driver of plant community assembly, as previously forecasted by studies focusing on pairwise interactions (e.g., Tielbörger & Kadmon 2000; Cavieres *et al.* 2006; Michalet *et al.* 2006), and indicates that this collapse is driven by the higher specialization of the species pool. Importantly, studies focusing on the relationship between facilitation and species richness that focused on pairings between dominant nurses and their neighbours did not find such facilitation collapse along similar aridity ranges as those studied here (Soliveres and Maestre 2014), although this collapse has been found in studies considering temporal variation in climatic conditions (Tielbörger and Kadmon 2000). This suggests that plant-plant interactions behave differently across environmental gradients depending on whether we focus on particular pairs of species (e.g., those including dominant shrubs) or in all possible pairs within a given community, and also on whether we focus on species richness or changes in relative abundances.

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Our results might explain why spatial patterns of dryland vegetation decouple from facilitation under aridity levels ≥ 0.8 (Berdugo et al. 2017a). Under these conditions, facilitation is no longer an important driver of species abundance, which is likely related to the size of plant patches. Previous studies have failed to link facilitation with ecosystem functioning (Maestre et al. 2010), probably due to the focus on the relationship between facilitation and species richness as the sole mechanism linking facilitation to ecosystem functioning (but see Mitchell *et al.* 2009). We speculate that focusing on the links between facilitation and species abundance, known to affect spatial patterns that are fundamental drivers of ecosystem functioning in drylands (Maestre et al. 2016), could provide the long hypothesized but largely untested link between facilitation and ecosystem functioning. Interestingly, at approximately the same aridity levels that facilitation declines and communities become more competition-driven, other studies have found important functional changes involving nutrient cycling rates (Wang et al. 2014) and drastic declines in ecosystem functioning (Berdugo et al. 2017a). Since plant-plant interactions are thought to affect ecosystem resilience (Kéfi et al. 2016), our study points that a possible driver of such sensitivity might be a shift from facilitation to competition-driven plant communities.

CONCLUDING REMARKS

The SDMs effectively isolated the effect of abiotic conditions, as supported by the good fit of estimated aridity optima of the observed community vs. the local aridity of each community (Figure 6.2a). The observed match between the relative importance of biotic/abiotic assembly drivers and patterns of height variation (Figure S 6.4) match predictions from theoretical approaches based on patterns of functional traits (Cornwell and Ackerly 2009, Mayfield and Levine 2010). Thus, the combination of approaches at different spatial scales introduced here effectively allowed us to isolate the role of abiotic conditions when analyzing the relative abundance of species within communities. We found shifts from facilitation- to competition-driven communities under aridity levels around 0.7, with potentially important cascading effects on ecosystem functioning that deserve further attention. Furthermore, by explicitly considering the adaptation of species to aridity we showed that facilitation was more important for maladapted species in drylands,

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and that specialized species pools stabilize the effect of environmental filtering across a large range of aridity levels. Our results emphasize the role of species adaptation to aridity as a modulator of the role of environmental filters and plant-plant interactions as drivers of community assembly. They also suggest that the composition of arid plant communities may be highly resilient to further increases in aridity, and that facilitation is key to preserve species less adapted to high aridity levels. These findings can be used to refine forecasts of plant community composition under climate change in drylands, the largest biome on Earth.

SUPPLEMENTARY FIGURES

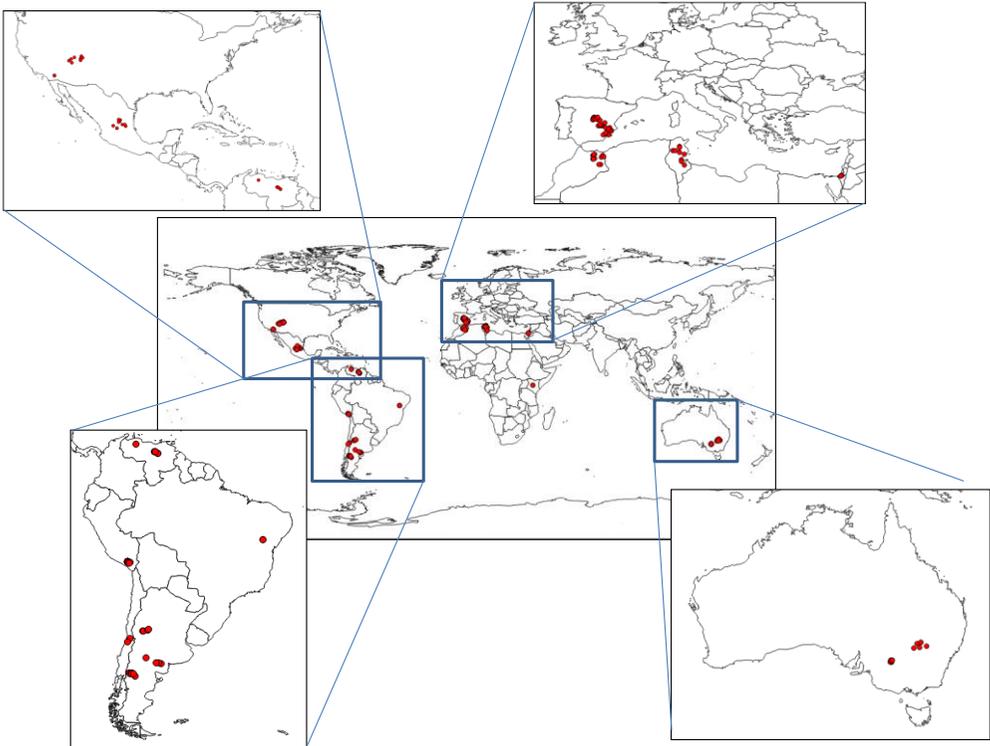


Figure S 6.1. Sites used in the study.
Map showing the geographical position of the 157 sites used in this study (red points).

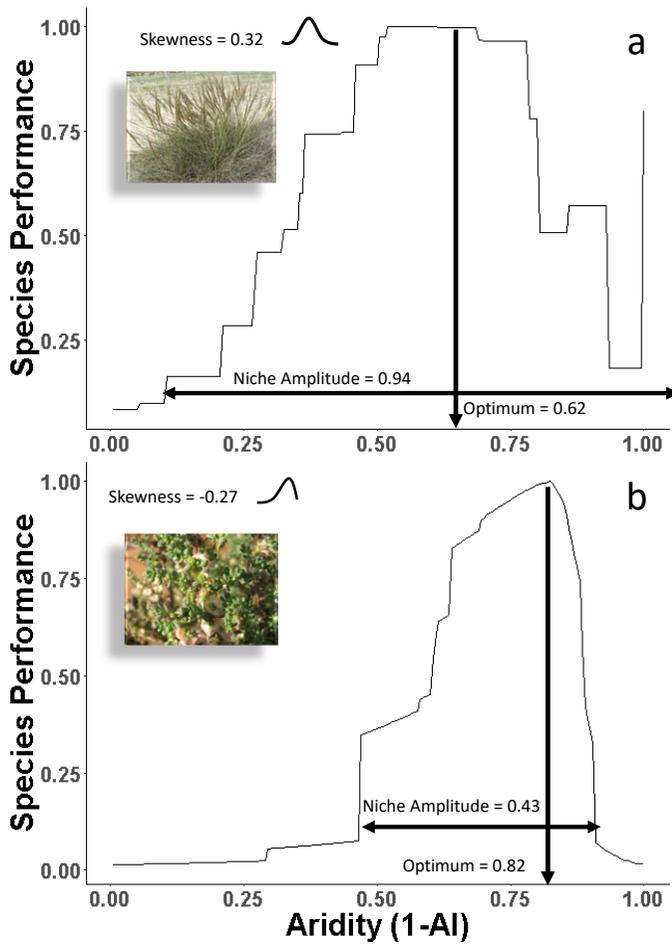


Figure S 6.2. Examples on niches.

Example of aridity niches for *Stipa tenacissima* (a) and *Maireana brevifolia* (b), including the features measured on them. AI = aridity index. Photographs of each plants are shown in the figure. Authors: a) Lumbar~commonswiki; b) BY-SA 3.0, downloaded from Wikipedia under creative commons license.

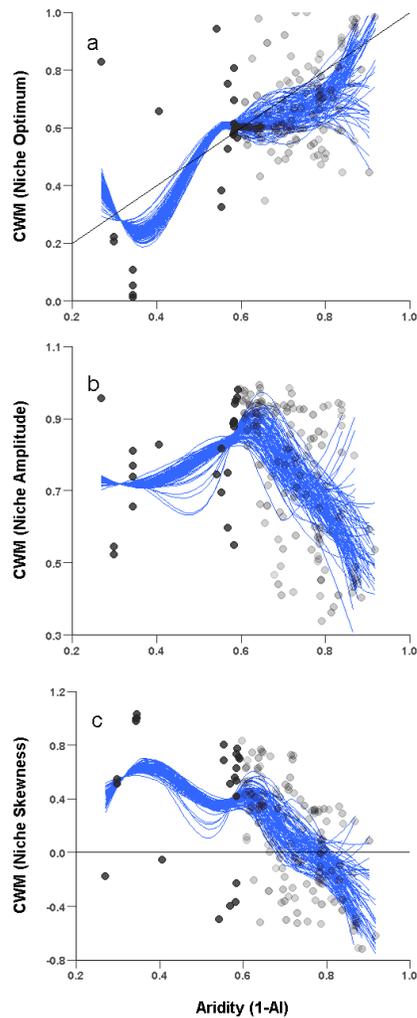


Figure S 6.3. Sensitivity analysis on niches through aridity.

Variation in the relationship between aridity and community weighted niche optimum (a), amplitude (b) and skewness (c) when using the same number of points at both sides of the intermediate aridity level of the study (Aridity = 0.6). We performed this regression 100 times by keeping the sites with aridity lower than 0.6 ($N=24$) and bootstrapping sites with aridity higher than 0.6 (so that total $N = 48$ for each regression). Each dot represents a community observed in one of the sites. The transparency of the data points is inversely proportional to the number of times the point was used. The blue line is the loess smoothed trend observed in each of the 100 bootstrapped samplings. The black line in a) represents the 1:1 line and in c) the 0 value, and indicates a change in the direction of skewness.

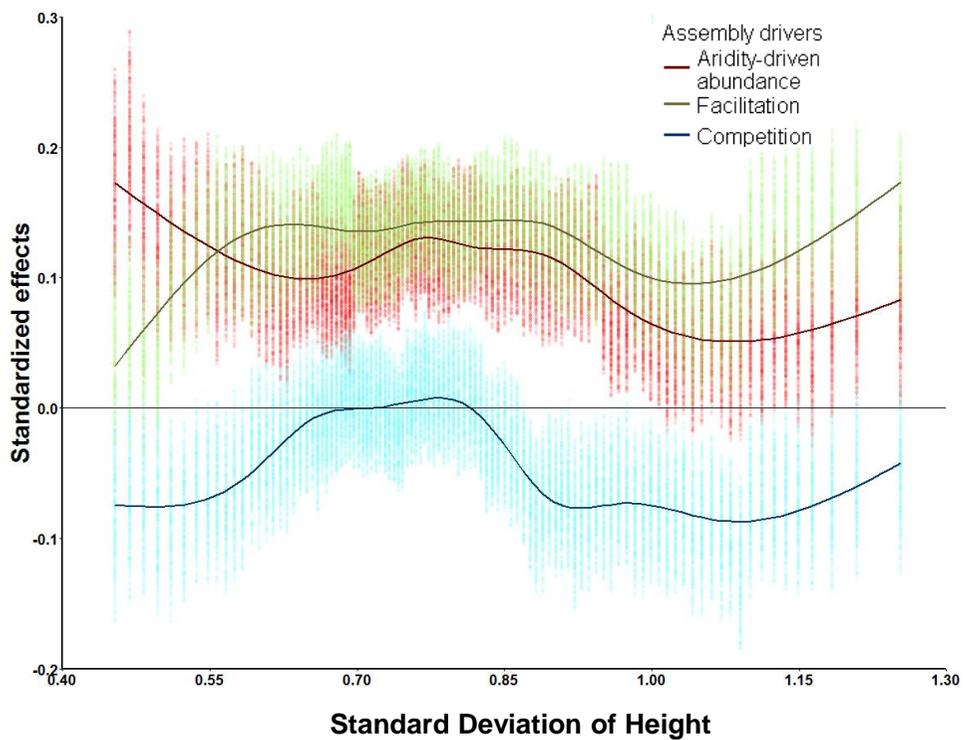


Figure S 6.4. Importance of assembly drivers through functional diversity gradient.

Standardized effects sizes of facilitation, competition and aridity along an aridity gradient. This analysis is performed by fitting a generalized mixed model (see equation 5) throughout a moving window subsetting our study sites following the gradient of height standard deviation within communities. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects.

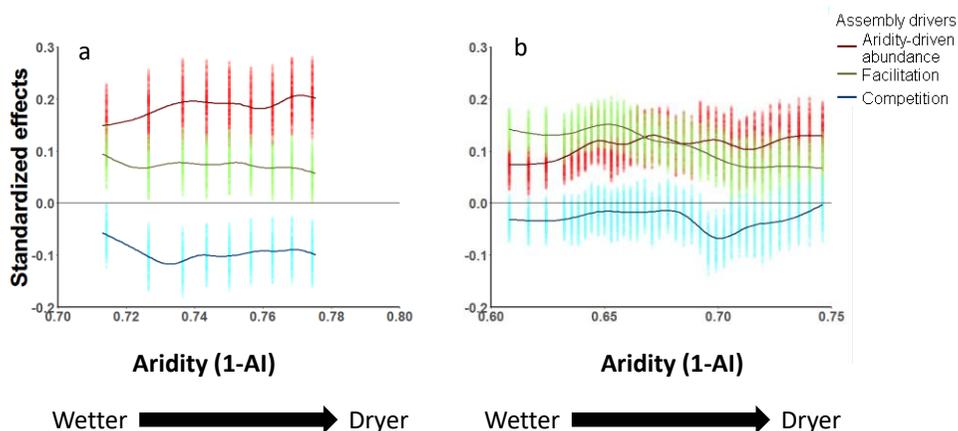


Figure S 6.5. Interaction of the importance of assembly drivers and gradients of aridity and specialization.

Standardized effects sizes of facilitation, competition and aridity along an aridity gradient for Specialized communities (CWSkewness <0, a), and not specialized communities (CWSkewness >0,b). This analysis is performed by fitting a generalized mixed model throughout a moving window (see figure 6.1d) in two subsets of our study sites according to CWSkewness. Bootstrapped coefficients of mixed models regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects.

Table S 6.1. Autoregressive models.

Results from a lineal and quadratic autoregressive model relating aridity and CW-Niche skewness with the importance of the different drivers of community assembly evaluated. The analysis takes the average of effect sizes per level of the contingent factor (as in Figures 6.4 and 6.5) as response variables and uses lagged values of these effects along the gradient at lags = 1 and 2 as covariates of aridity/CW-Niche Skewness to control for autocorrelation. Int. Facil: interaction of Aridity-driven abundance and facilitation. Int. Compet: interaction between Aridity-driven abundance and competition.

	Assembly driver	Slope	Quadratic term
Specialization	Aridity-driven abundance	-0.01*	-0.03 (n.s.)
	Facilitation	-0.01 (n.s.)	0.02 (n.s.)
	Competition	-0.01 (n.s.)	0.02 *
Aridity	Aridity-driven abundance	-0.01 (n.s.)	-0.50*
	Facilitation	-0.16***	-0.08(n.s.)
	Competition	-0.09*	-0.04 (n.s.)
	Int. Facil	0.00 (n.s.)	0.15 (n.s.)
	Int. Compet.	0.82*	-0.55 *

Note: *** significant at $P < 0.001$, ** significant at $P < 0.01$, * significant at $P < 0.05$, • marginally significant, (n.s) not significant

APPENDIX 3.1: EXTRACTION OF SPECIES NICHES CURVES

Occurrence data

We downloaded species occurrences (i.e. presence data) of the 898 species found in the drylands surveyed from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>). GBIF offers a free and comprehensive database of different species all over the world, including their synonyms, growth form, and occurrences. Despite some limitations of GBIF data (Beck et al. 2013, 2014), this database is commonly used to extract species occurrences and to build species distributions models (SDMs, see Deblauwe et al. 2016, Gomez & Cassini 2015, Leiblein-Wild et al. 2015).

We removed the occurrences that either did not lay on earth ground (i.e. data that are not properly georeferenced) or were considered outliers according to the bulk of occurrences found. For doing the latter, we calculated the centroid of all occurrences for each species, and calculated the Euclidian distance between each occurrence and the centroid. We removed those occurrences that fell out of the 95% confidence interval of the distance probability density function if two conditions were satisfied: i) they were separated by more than 500 km from the centroid, and ii) they occurred further than 500 km from the nearest conspecific. By doing this outlier identification, we avoid accounting for single occurrences far from the species distribution centroid or far from a particular distribution cluster. The threshold used here (500 km) is sufficiently rare for plants to accomplish a frequent (1 event each 10 years) and/or successful (probability of seed arrival $\approx 10^{-20}$; probability of seed survival $\approx 10^{-4}$) dispersal process, even being within the range of distances for which the probabilities of seed dispersal are impossible to estimate with current methods due to their low values (Nathan 2006).

Because the sampling effort of data from GBIF varies depending on the geographical area considered, we used a resampling method to remove points that were too close to each other (Phillips *et al.* 2009; see also Berdugo et al., 2016 for the code used to perform this task automatically). We discarded all occurrences falling within 10 arc-minutes (≈ 18.5 km) distance from another. There is no specific method in the literature to select the threshold of grid size that best avoids sampling bias effects, especially when dealing with that many species. So, we selected 10 arc-minutes as it maximizes the relationship between the curves of

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species remaining versus minimum number of occurrences needed to perform SDMs and the grid size (Figure SA 6.1).

Extracting niches

To model the aridity niches of the species studied, we used MAXENT (Dudik et al. 2004) with the “dismo” library (Hijmans et al. 2015) in R (R Development Core Team 2008). The methods and rationale of MAXENT rely on the fact that the environmental envelope depicting the points in which a species is occurring is the conditional probability of the environment given that the species occurs there (i.e., $P(\text{environ}|1)$). To extract the probability of the species occurrence given a certain environmental condition (and thus its environmental niche), the Bayesian principle might be used as follows:

$$P(1|\text{environ}) = \frac{P(\text{environ}|1) \cdot P(1)}{P(\text{environ})}, \quad \text{equation S 6.1}$$

where $P(1)$ is the probability of the species to occur independently of the environmental condition (which is a surrogate of prevalence for that species) and $P(\text{environ})$ is the probability distribution of the environment. This equation can be scaled to the prevalence of the species, giving a species sensitivity index equivalent to assuming all species being equally prevalent (i.e., being their occurrence only dependent on the environmental conditions irrespective of whether they are rare or not), as follows:

$$\frac{P(1|\text{environ})}{P(1)} = \frac{P(\text{environ}|1)}{P(\text{environ})} \quad \text{equation S 6.2}$$

Only $P(\text{environ}|1)$ and $P(\text{environ})$ are required to estimate this sensitivity index. $P(\text{environ}|1)$ can be extracted from GBIF data since it is the frequency distribution of each species' occurrence according to the environmental predictor(s) chosen (aridity in our case). The estimation of $P(\text{environ})$ is the description of a geographic envelope of the abiotic variable of interest (called background sampling and representing the environmental conditions offered to the species within the region of study). In other words, we calculate the relative performance of a species as a relativized estimation of the aridity values in which it is found respect to how

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abundant are these aridity values within the study region. For this, we used the ecological realms (“ecozones”) described by Pielou (1979) and Udvardy & Udvardy (1975) as environmental envelopes (<http://www.worldwildlife.org/biomes>). This is a broad, generally accepted and meaningful eco-geographical division that accounts for the evolutionary history of the plants (Udvardy and Udvardy 1975, Dixon et al. 2014, Elder et al. 2016). Therefore, we assume that each species has an environmental envelope corresponding to the aridity values of the bioclimatic zone in which it is living. We sampled 1000 points randomly throughout each ecological realm to use them as background sampling. MAXENT used these points to extract the environmental envelope from the maps. We classified each species according to the ecological realm they occupy, and for each species added the corresponding background sampling. In the case that more than one realm was occupied, we added background sampling from as many realms as were occupied by the species, so that no more than 1000 points were introduced as background sampling anyway. The envelope entails a correction of the environmental availability for the species. For instance, it corrects for the fact that a given set of environmental conditions are infrequent in nature.

Provided the background sampling and species occurrences, MAXENT uses a machine-learning procedure to estimate the response curve of niche adequacy based on equation S1 (see Elith et al. 2011 for a review). MAXENT uses different combinations of linear, product, quadratic, hinge, threshold and categorical fitting (called features) during this machine-learning procedure, and calculates the estimates of the coefficients of these different fittings. Then, MAXENT calculates the log likelihood of the different fittings and penalizes both the number of parameters and the number of features used in the fitting procedure using a method called regularization (Tibshirani 1996). MAXENT maximizes the penalized log likelihood, which is equivalent to minimize the relative entropy of the model affected by error-bound constraints, to provide the niche.

We retained only those species for which we had at least 20 occurrences ($N = 701$), as this threshold has been identified as sufficient to account for rare species in SDMs (Williams et al. 2009, Gogol-Prokurat 2011). We used the area under the curve method (AUC) to validate the niche fitted. This method separates 10% of the occurrences to perform a validation process of the niche. Validation is performed

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by predicting the probability of occurrence of the species throughout the study region based on the niche and testing whether the cases saved for validation satisfy the occurrence patterns predicted by the niche (Raes and ter Steege 2007). AUC is similar to an R^2 metric, as it ranges 0 to 1 and indicates the fitting of the model to the observed data. The AUC found in the study for the 701 species are displayed in Figure SA 6.2. We normalized these curves to the maximum value of niche adequacy, thus ranging between 0 and 1 in the y-axis (species performance), to use it for interpolations in the rest of analyses. Figure S 6.3 shows two examples of the aridity niches obtained, as well as of the features we measured on them.

Appendix figures

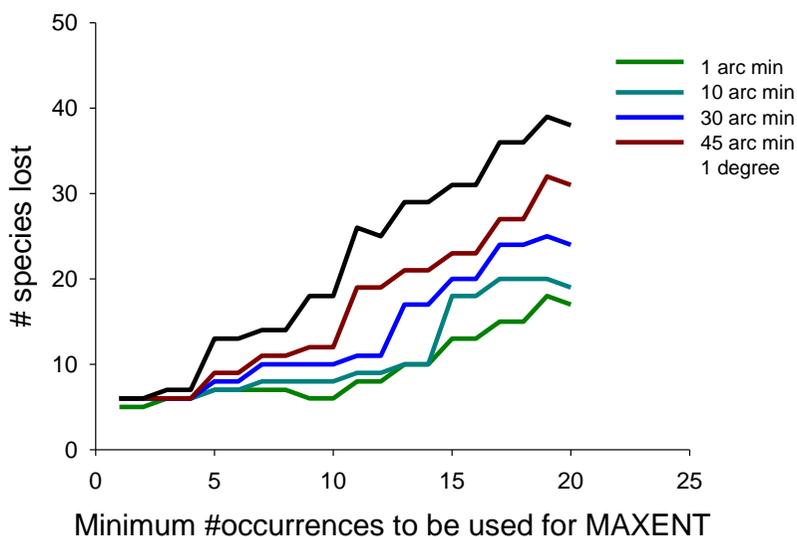


Figure SA 6.1. Dependence of number of species with spatial resolution used on sampling bias

Number of species that would be lost versus the minimum number of occurrences required to conduct species distribution models for different thresholds of grid sampling bias. Grid sampling bias indicates the size of a grid within which occurrences of species are considered to be the same occurrence. We selected 10 arc minutes as it represents the curve that best maximizes the number of species remaining with the widest grid size.

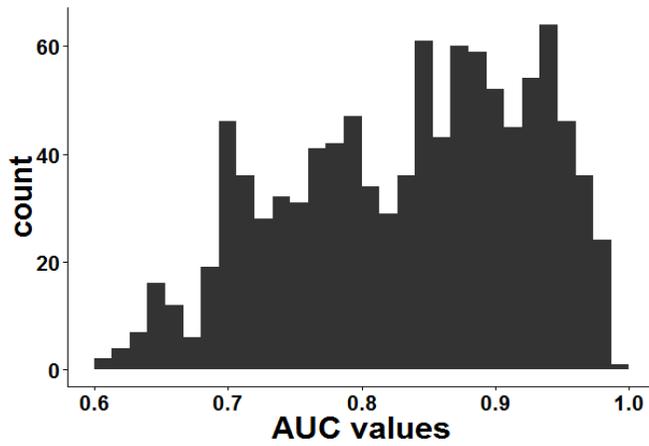
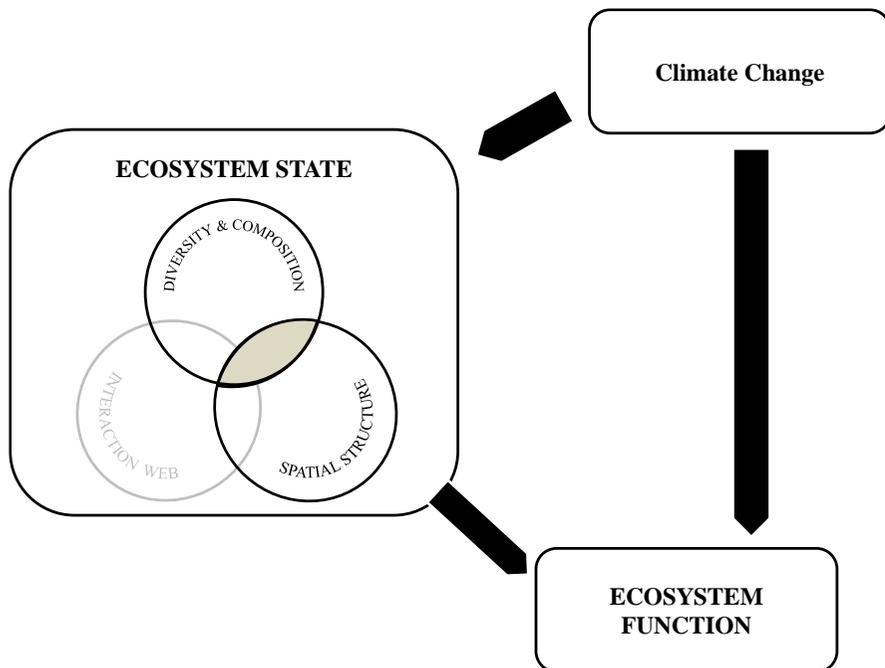


Figure SA 6.2. AUC values found

Absolute frequency histogram of area under the curve (AUC, a validation index of aridity niches scoring 0 to 1 similarly as R2 coefficients) values of MAXENT outputs for the 701 species used in this study.

Community specialization associates with the existence of several multifunctionality states in global drylands



Miguel Berdugo, Nicolas Gross, Santiago Soliveres, Sonia Kéfi, Yoann LeBagousse-Pinguet, Fernando T. Maestre

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ABSTRACT

Community composition is a key attribute of communities that is related to other important community features such as spatial patterns and ecosystem functioning. Empirical and theoretical studies have linked changes in spatial patterns of vegetation to alternative multifunctionality (i.e. the ability of providing different ecosystem functions simultaneously) and degradation states in ecosystems such as drylands, which cover over 45% of terrestrial surface. However, we do not know whether shifts in community composition are related to this association. Here we used a global dryland survey to explore the links between multifunctionality states, the specialization of dryland plant communities to aridity and the spatial pattern of vegetation. We found that the specialization of communities explains the association between the spatial pattern and multifunctionality states. We associated specialization of the communities with a change in the strategy of plants to face aridity, from stress tolerance to stress avoidance occurring at aridity levels around 0.7. This threshold concurs with that shown in chapter 3 in which facilitation is no longer a key assembly driver of communities. Thus, our results point that this shift in the association of trait syndromes to community specialization may affect profoundly the nutrient additions to the soil and the type of dynamics that dryland ecosystems exhibit at both sites of this aridity threshold. Per our results, plant species highly adapted to aridity which will increase their global extent by about 60-200% by the end of this century because of widespread increases of aridity with climate change. This will entail drastic losses of ecosystem functioning in global drylands, where a good part of their population relies on ecosystem services for their livelihood.

Keywords: Specialization, alternative states, spatial pattern, multifunctionality, community composition

INTRODUCTION

Drylands, defined as areas where the aridity index (ratio precipitation/potential evapotranspiration) is lower than 0.65 (Middleton and Thomas 1992), constitute the largest biome on Earth (ref), and are an excellent natural laboratory to study changes in the composition of ecological communities along gradients of environmental harshness (refs). Shifts in species composition have been reported several times along regional (Fernandez-Going et al. 2013, Ferrenberg et al. 2015) and global (Ulrich *et al.* 2014) aridity gradients, and sometimes may happen in abrupt ways at particular aridity thresholds (Ulrich et al. 2014). Species develop different ways of coping with environmental harshness (Wright et al. 2004, Martínez-Cabrera et al. 2009, Gleason et al. 2013), and therefore shifts in community composition might be related to ecophysiological thresholds related to the way in which plants adapt to aridity. Indeed, recent developments on statistical tools such as species distribution models allow to examine the way in which species adapt to aridity by examining the shape and features of their niche (Elith and Leathwick 2009). Using these techniques, Berdugo et al. (Chapter 3), showed that the whole community in drylands specialize to aridity (i.e., species whose optimum occur at high aridity sites rather than in low aridity sites become dominant in the community) at aridity values around 0.7 (calculated as 1- aridity index). However, they did not investigate the link between abrupt community shifts and the characteristics of the species involved (e.g., by examining changes in trait syndromes), which might provide key insights about the mechanisms involved in the shifts in the identity of the species living in dryland community with increasing aridity.

Importantly, changes in the composition of communities might largely affect the ecosystem functioning. Community trait composition, in particular, has been linked to the ability of ecosystems to control functions such as nutrient cycling and productivity (see, for instance (Lavorel and Garnier 2002, de Bello et al. 2010), and to provide several of these functions simultaneously (multifunctionality, e.g., Valencia *et al.* 2015; Gross *et al.* 2017). For instance, communities with higher specific leaf area (SLA) and taller plants generally produce more biomass and show higher rates of nutrient cycling than those with opposite traits (Lavorel and Garnier 2002). Also, although the ability of species to tolerate aridity has been related to some trait syndromes (e.g., tolerant species have

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lower SLA and height, Cornwell & Ackerly 2009; Gross *et al.* 2013), there is no study relating niche specialization with functional traits across global aridity gradients in drylands. Because both the effects of community traits on multifunctionality and the shifts in these traits due to changes in environmental conditions occur simultaneously in nature, and because widespread increases in aridity are forecasted for the coming decades due to climate change (Huang *et al.* 2015), studying the link between community specialization, aridity increments and ecosystem functioning will provide important insights to understand changes in ecosystem functioning with climate change.

Responses of multifunctionality to increases in aridity in drylands are likely to be non-linear. Indeed, drylands are iconic ecosystems for study abrupt transitions, as multiple studies have shown that increases of environmental harshness might entail profound and sudden shifts in ecosystem properties that might be hardly reversed once they happen (Kéfi *et al.* 2007a, Bestelmeyer *et al.* 2015, van Nes *et al.* 2016b). In this regard, a recent study found alternative stable states in multifunctionality that coexist through aridity gradients in global drylands (Berdugo *et al.* 2017a). The authors linked the existence of both multifunctionality states to a shift in the dominant spatial patterns of vegetation. One of the spatial patterns fitted power law functions ('PL-like', associated to high multifunctionality states in global drylands) and another was characterized by distributions similar to lognormal (nonPL-like, associated to low multifunctionality states; (Berdugo *et al.* 2017a). Interestingly, changes in multifunctionality state and spatial patterns both occurred at aridity thresholds around 0.7, which matches that found for the specialization of communities in global drylands (Chapter 3). Thus, community shifts might be playing a role in the existence of this threshold.

The role of community composition on controlling the spatial pattern of vegetation has seldom been studied. Some studies have linked the existence of certain spatial patterns to some properties of the dominant species such as the clonal reproduction exhibited by certain functional types (Lett and Knapp 2003, Ravi *et al.* 2008). The study by Berdugo *et al.* (Chapter 3) suggested another way in which community shifts might be controlling spatial pattern. In that study, the specialization of communities to aridity was related to the waning of the importance of facilitative interactions at the whole community level. This occurs probably because of the tight dependence existing between plant-plant interactions

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and the type of species living in a community, particularly regarding the adaptations they have to cope with environmental stress (Liancourt *et al.* 2005; Gross *et al.* 2010; Soliveres *et al.* 2012). Facilitative-driven ecosystems are characterized by power law-like patch-size distributions (Von Hardenberg *et al.* 2001, Kéfi *et al.* 2007b, Scanlon *et al.* 2007, Berdugo *et al.* 2017a), while competition-driven ecosystems are characterized by a typical patch size (Manor and Shnerb 2008a, Xu *et al.* 2015a). Thus, there might be a link between community specialization and spatial patterns of vegetation that has still not been explored. Whether this link can explain the bistable nature of multifunctionality observed in drylands (Berdugo *et al.* 2017a) remains totally unexplored, and its study will shed light on our understanding of the mechanisms underlying abrupt changes in multifunctionality with climate change.

Understanding how community specialization relates to shifts in multifunctionality and plant spatial patterns may not only help explaining the mechanisms involved in aridity thresholds of those variables, but it also introduces a new tool for forecasting those shifts in the context of ongoing climate change. By examining the range of environmental conditions in which species live, it is possible to estimate their climatic envelope and forecast how their distribution would change in space with future climatic predictions (Elith & Leathwick 2009). Such predictions might imply the possibility of forecasting where and when shifts in community composition are more likely to occur through species responses to climate change, and making educated guesses on how spatial patterns and multifunctionality may shift with them.

Here we aim to study how community specialization in drylands relates to the link between plant spatial patterns and multifunctionality types in global drylands as well as predicting species specialization with climate change. To do so, we used field data gathered from drylands in all continents except Antarctica and conducted a three-step analytical approach. First, we investigated the relationship between community specialization and plant spatial patterns and its relationship with multifunctionality alternative states in drylands. Then, to shed light on possible mechanisms driving these changes, we conducted analyses to find which plant trait syndromes are associated to the shift in community specialization observed in global drylands around aridity levels of 0.7. Finally, we used species distribution models to assess how changes in the ranges of specialized species may

occur with ongoing climate change, thus providing clues about future scenarios of these shifts in species composition.

MATERIAL AND METHODS

Study Sites

For this study we used a subset of the 236 dryland ecosystems available from the EPES-BIOCOM database (Maestre et al. 2012a, Ulrich et al. 2016). These sites encompass a wide range of the environmental conditions that can be found in drylands today, with total cover varying from 3 to 82 %, aridity (calculated as $1 - \text{aridity index}$; the latter extracted from Zomer *et al.* (2008) ranging between 0.27 and 0.92, species richness between 2 and 46, and a large variation in species composition (the studied sites encompass multiple types of grasslands, shrublands and savannas/open forests).

These sites were surveyed between 2006 and 2013 using a standardized protocol (Maestre et al. 2012a). At each site, four transects of 30-m long were displayed, separated by 8 m from each other, always facing equator and downslope. We established 20 quadrats (2.25 m²) along each transect (80 per site) and estimated the cover of each perennial plant species. We identified a total of 898 species to the species level in this survey, and, when possible, we extracted information on their height and specific leaf area from previous studies, local floras and global databases (Kleyer et al. 2008, Kattge et al. 2011). See Soliveres *et al.* 2014; Le Bagousse-Pinguet *et al.* 2017a and cite:cosmic for more details on trait data acquisition. At each site, we also collected five soil cores (0-7 cm depth) in areas close to the transects and devoid of perennial vegetation. After collection, soils were sieved (2mm mesh), air-dried for one month and stored for laboratory analyses. All soil samples were shipped to Spain to standardize soil analyses and in the same laboratory.

Multifunctionality extraction and calculation

We analysed 16 soil chemical properties related with the carbon (C), nitrogen (N) and phosphorous (P) cycles (hereafter referred as functions). The functions include: organic C, beta-glucosidase activity, pentoses, hexoses, aromatic compounds,

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phenols, nitrate, ammonium, total N, potential N transformation rate, amino acids, proteins, available P, phosphatase activity, inorganic P and total P. A complete methodology on the measurement of each one of these functions can be found in Maestre *et al.* (2012) and Delgado-Baquerizo *et al.* (2013). These functions are well known surrogates of soil fertility in drylands (Whitford 2002), and have been used previously in studies about ecosystem functioning (Gamfeldt *et al.* 2008, Isbell *et al.* 2011, Maestre *et al.* 2012a). Furthermore, most of these functions are also considered to be supporting ecosystem services, as other types of ecosystem services, such as the production of plant biomass and livestock, depend on them (Millennium Ecosystem Assessment 2005, Balvanera *et al.* 2006, Isbell *et al.* 2011). To calculate multifunctionality values, we normalized all functions and calculated the average of those normalized values (i.e., ability of supplying several functions at the same time, see Hector & Bagchi 2007; Maestre *et al.* 2012; Byrnes *et al.* 2014). This multifunctionality metric is an average of soil properties linked to nutrient cycling of C, N and P. Since all the functions measured have been associated positively to ecosystem functioning of dryland soils, high multifunctionality values always would be related to higher fertility of soils and vice versa.

Bimodality in multifunctionality

Using the same database used here, multifunctionality was shown to follow a bimodal distribution (Berdugo *et al.* 2017a). Bimodality has been interpreted as a hint for alternative stable ecosystem states (stable states should be observed more often in ecosystem snapshots taken at different locations but with otherwise similar environmental conditions, see Livina & Lenton, 2007; Hirota *et al.*, 2011; Scheffer *et al.* 2012). We used the same approach as Berdugo *et al.* (2017) to find the potential landscapes of multifunctionality in the subset of sites used here (note that are not the same as used by Berdugo *et al.* 2017 due to the availability of plant trait data). A potential landscape is defined here as a transformation of the multifunctionality histogram in which the most frequent values are assumed to reflect the most stable states (Livina and Lenton 2007). Obtaining potential landscapes entails: i) performing gaussian-mixture analyses to validate the bimodal pattern; ii) transforming the histogram by applying the following equation:

$$U' = -\frac{\sigma^2}{2} \log(\text{PDF})$$

equation 7.1

where, σ^2 is the level of noise in the system, PDF is the Probability Density Function derived from the dataset by using a kernel smooth function (*density()* function in R with bandwidth, $h = 1.06 s/n^{0.2}$ with s being the standard deviation of the data and n the number of data points). By calculating the scaled potential (U'/σ^2), we do not need to estimate the level of noise of the system. We used the `multmixmodel.sel()` function from `mixtools` package from R (Benaglia et al. 2009) to calculate the Akaike and Bayesian information criteria estimates (AIC, BIC) for one and two modes in the multifunctionality values. In this procedure, the highest AIC/BIC values indicate the best fit (Figure S 7.1).

Calculation of aridity niches and CWM Skewness as a metric of community specialization

We used species distribution models (SDMs) to calculate the niches of species found in the sites surveyed. SDMs are logistic models relating the occurrences of species (response variable) and climatic variables (predictors) using non-linear techniques (Elith and Leathwick 2009). We extracted occurrences of species from the Global Biodiversity Information Facilities (GBIF), and used aridity maps from Zomer *et al.* (2008) as predictors. We performed SDMs as described in (Chapter 3) using MAXENT (Elith et al. 2011) with the `dismo` package (Hijmans et al. 2015) in R (R Development Core Team 2008). The results of these models are comparable to probability distributions of species occurrences along global aridity gradients (i.e., realized niches *sensu* Hutchinson, 1957, see also Soberón, 2007), and contain information on the adaptive strategies of the species regarding aridity. Specifically, we extracted the specialization to aridity of species by measuring the skewness of those distributions as described in (Chapter 3). Skewness indicates the asymmetry of the niches and, when this asymmetry pushes maximum developments of species in high aridity values (negative skewness) we can consider that those species developed marked preferences for arid conditions. Also skewness has been found to relate to niche breadth (Chapter 3), which is a standard metric of specialization in biogeography (i.e., adaptation of species to particular and constrained conditions Devictor *et al.*, 2010). We think that niche breadth is misleading when used as a metric to quantify the specialization to aridity for two reasons: i) the range of

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aridity values that a species encompasses does not inform about the aridity preferences of the species; ii) low aridity values have an asymptotic effect on plants, as aridity levels/values equal to 0 (i.e., Ppt/PET = 1) have similar effects on water availability for plants than aridity levels/values lower than 0 (i.e., water is no longer a limiting resource), therefore niche breadth does not mean the same in low than in high aridity ranges. Thus, we always refer to niche skewness when talking about specialization. Niche skewness summarizes both niche breadth and adaptation to high aridity values, and is a good indicator of marked preferences for arid conditions of a species; moreover, the interpretation of this metric is straightforward (lower than 0 means right skewed niches, thus species preferences for arid sites more than for wet sites). For community-level measurements of specialization, we used the skewness of the distributions as a feature of each species and calculated community weighted means of skewness (CWM Skewness) of all species (adapted from Lavorel & Garnier, 2002). This metric informs about the dominant plant strategy regarding specialization in a community (negative if specialized). We could retrieve information from about 157 communities, in which niche skewness information was available for species summing up to at least 60% of the total perennial cover (Chapter 3).

Measurement of patch-size distributions

To measure spatial patterns of vegetation, we used the power law range descriptor developed by Berdugo *et al.* (2017). This metric quantifies the percentage of a given patch size distribution that fits power law functions, which is highly related to the shape of patch-size distributions. Low values of this metric indicate curved distributions (e.g. fitting lognormal distributions), whereas high values indicate distributions that mostly fit a power law. Patch sizes were extracted from classified aerial images of the sites surveyed and power law functions were fitted using (Clauset *et al.* 2009) methods. Power law fitting yields two main parameters: α (decay rate of frequency with patch-sizes) and x_{min} (patch size from which power law is considered a proper fit). Because x_{min} can be very high, sometimes the range of patch sizes that fit power laws are not representative of the overall shape of the distribution. Hence, the power law range descriptor is aimed at measuring the suitability of power law fitting to the data. It is calculated as:

$$\text{Power Law Range} = 1 - \frac{(\log_{10}[x_{\min}] - \log_{10}[x_{\text{smallest}}])}{(\log_{10}[x_{\max}] - \log_{10}[x_{\text{smallest}}])} \quad \text{equation 7.2}$$

where, x_{\min} is the patch size from which the power law is fitted; x_{\max} is the maximum patch size of the distribution and x_{smallest} is the smallest patch size found in the distribution. Therefore, the ratio in the equation represents how large is the range that does not fit a power law (from x_{smallest} to x_{\min}) with respect to the entire range of the distribution (x_{smallest} to x_{\max}).

Importantly, two main types of distributions have been found in drylands using the power law range metric: distributions with power law range values score higher than 0.57 (i.e. PL-like distributions), are considered fundamentally different from those scoring lower than 0.57 (i.e. nonPL-like distributions). This classification is based on the drivers of the shape of path-size distributions (facilitation in the case of PL-like and community weighted mean of height in nonPL-like), as well as on the ability of patch-size distributions to maintain scale-invariant properties (see Berdugo *et al.*, 2017 for details). In this study we directly used the type of patch-size distribution (PL-like, nonPL-like), as these types have been related categorically to multifunctionality types (Berdugo *et al.* 2017a). We obtained the data from a subset of sites of the study of Berdugo *et al.* (2017), where additional information on the procedure for image classification and power law fitting can be found.

Statistical analyses

Predicting multifunctionality with community specialization and spatial pattern

We used generalized linear models to assess the effects of community specialization and spatial patterns on multifunctionality. As this analysis evaluates whether specialization and spatial pattern may be able to distinguish multifunctionality types (thus accounting for the existence of alternative multifunctionality states), multifunctionality was categorized according to threshold values based on previous literature. Multifunctionality was divided into high functional type and low functional type depending on whether its value was higher or lower than the unstable state detected in the potential analysis (see previous section and (Berdugo *et al.* 2017a)).

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We conducted four models with different predictors. In model 1, we assessed the association between spatial patterns and multifunctionality alone. This was performed to ensure that this association is maintained, as predicted in Berdugo et al. (2017), for the subset of sites used here (constrained by data availability on plant spatial patterns and community specialization, N = 98). In model 2, we also included community specialization and its interaction with aridity to assess whether plant spatial patterns remained significant when adding this variable. We introduced this interaction because the specialization of communities is strongly related to aridity (Chapter 3). In model 3, we included total cover and species richness to assess whether significance of community specialization and spatial patterns remained after accounting for two well-known multifunctionality drivers (see Maestre *et al.* 2012; Delgado-Baquerizo *et al.* 2013). Species richness is known to drive multifunctionality in global drylands (Maestre et al. 2012a) and we included aridity and cover as covariates in this analysis because they strongly influence both spatial patterns and community specialization (see Chapter 3 and (Berdugo et al. 2017a)) and are well known to also affect ecosystem functioning. Finally, in model 4 we discarded spatial pattern of vegetation to increase the statistical power of our analysis (N=157) and explore further the significance of community specialization on driving multifunctionality types.

All these analyses were done using a binomial distribution as an error distribution model (as multifunctionality was always categorical with two factors). We used the function `glm` in R to do these analyses.

Evaluating the response of specialization, spatial pattern and multifunctionality to aridity increments using potential analysis

Because multifunctionality, community specialization and spatial patterns might exhibit contrasting alternative states (Berdugo *et al.* 2017), we wanted to assess whether these stable states (understood as the most frequent values, see section bimodality in multifunctionality above) vary through aridity gradients exhibiting either one or several alternative states. To do so, we used potential analysis using a moving window through aridity. First, we used a subset of the 30 less arid sites of the database (corresponding to approximately one third of the total N, see (Berdugo et al. 2017a)) and performed potential analysis as described above. Then we iteratively discarded the less arid site and added the next more arid up to the most

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arid site in the dataset. We extracted the value of stable states (minimum in potential landscape as in Figure 7.1, see (Livina and Lenton 2007, Hirota et al. 2011, Berdugo et al. 2017a)), and plotted it through the aridity values obtained in the moving window (mean of the different subsets). If bimodal, two points were plotted for the same aridity value, thus indicating the existence of alternative states co-occurring at these aridity levels.

Predicting community specialization with functional traits

To test how skewness was related to functional traits, we built a model using the community weighted means of specific leaf area and of plant height for the subset of sites where this information was available for species accounting at least for 60% of total plant cover (N = 116). The model was built as:

$$\text{CWM Skewness} \sim \text{CWM(SLA)} * \text{CWM(H)} * \text{Aridity} \quad \text{equation 7.3}$$

where CWM Skewness is the measurement of specialization, and CWM of height and specific leaf area where determined by the same method used for niche skewness and specialization with the values of height and SLA (see "Calculation of aridity niches and CWM Skewness as a metric of community specialization" above; and Lavorel & Garnier, 2002). We introduced interactive terms in the model because plant trait strategies have been found to change along regional aridity gradients (Gross et al. 2013, Valencia et al. 2015), hence the relationships between community specialization and functional traits may vary depending on the aridity level considered. We also assumed an interaction between SLA and height to account for possible trade-offs between these traits (Suding et al. 2003, Cornwell and Ackerly 2009).

To better visualize the interactions of the model, we adopted a moving window approach using a simplified version of the model shown in eqn 3 without aridity. To do so, we first used the 30 most humid sites (as this N provided sufficient statistical power to fit two interacting predictors, see Moore 2010) and fitted the model (without aridity) to these sites. We extracted bootstrapped values of model coefficients. We then discarded the most humid site and added the next

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most arid site iteratively repeating the procedure up to the addition of the most arid site in the database. This procedure allowed us to show changes in the effect of traits on specialization in a continuous way.

To evaluate whether the patterns observed correspond to certain types of communities, we repeated the analyses but splitting the dataset according to habitat types. We classified sites as grassland (N = 55), shrublands (N = 61) and open forest-savannahs (N = 18). In this latter case, we could not retrieve enough number of sites to perform the moving window analyses, thus these results were not displayed.

Expansion of specialists with climate change

To select potential species that might be indicating specialization of a community, we obtained the aridity specialist species (i.e. those species with niche skewness <0) that were present in the sites surveyed and that had a relative abundance of at least 10% (corresponding to the 30% most dominant species in the dataset).

SDMs can be used to forecast changes in the distribution of species. By knowing the relationship between species occurrences and aridity, SDMs allow us to extrapolate how species niches would look under future climatic conditions based on climate change forecasts. The outputs of such extrapolations are usually displayed in the form of habitat suitability maps, rendering the probability of the species to occur in different sites of the region of study. We used maps of aridity forecasts taken from ref: (Huang et al. 2015) to extrapolate our resulting MAXENT outputs of the species identified as potentially dominant and specialists. We displayed the results of scenarios of representative concentration pathways (RCP) 4.5 (scenario in which CO₂ emissions meet saturation around 2060) and 8.5 (scenario where CO₂ emissions are hypothesized to increase exponentially during the simulation period), as the difference between the maximum habitat suitability for the 41 species under aridity conditions found in 2012 and 2100 (aridity data were taken from Huang *et al.* 2015). Therefore, the maps show whether any of the 41 species studied is expected to increase or decrease their habitat suitability globally with climate change. In these analyses, we only considered habitat suitability increases occurring within the ecological realm in which target species exist currently. Therefore, we are assuming that dispersal limitation occurs at the realm scale (i.e., plants cannot disperse between realms, for instance, habitat

suitability increases in China plants from South America are not considered, see Udvardy & Udvardy 1975; Dixon *et al.* 2014; Elder *et al.* 2016) and we are not taking into account potential human dispersion of these species.

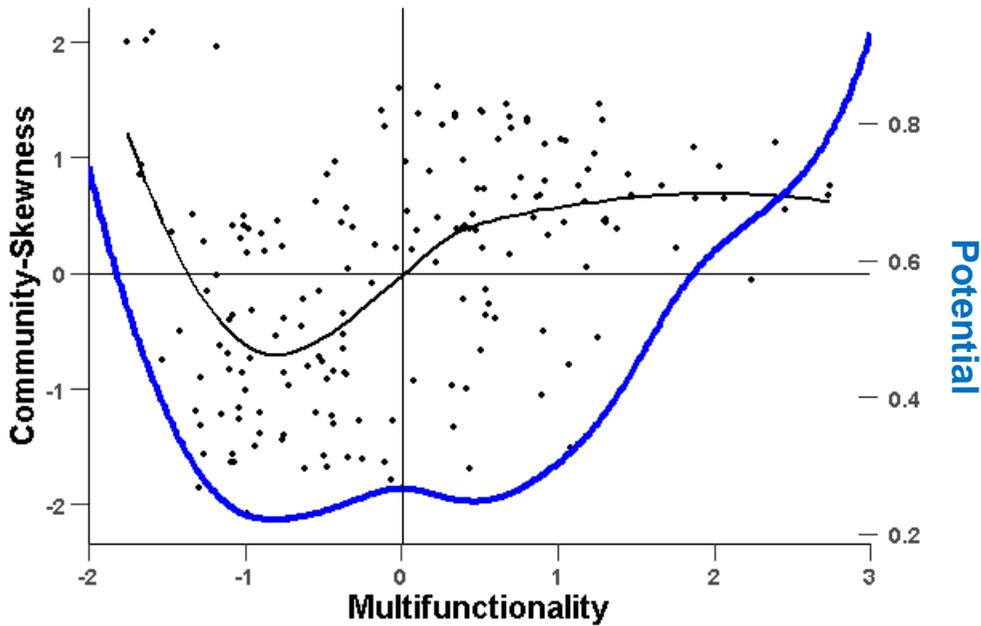


Figure 7.1. Community specialization relates to multifunctionality stable states.

Match between community specialization and multifunctionality states in global drylands. The blue line represents the multifunctionality potential, where local minima are the stable states (right axis). The vertical line marks the local maxima of multifunctionality (separating the two multifunctionality types, see methods). Community specialization is measured as community weighted mean skewness, thus negative values indicate dominance of right-skewed niche species. Horizontal line marks the 0 value of community skewness. The black line represents the gam-smoothed trend of community specialization.

RESULTS

Relationship between community specialization, plant spatial patterns and multifunctionality states

Although spatial patterns were initially associated with multifunctionality types (Model 1, Table 7.1), this association disappeared when community specialization was added in the model (Model 2, Table 7.1). Community specialization effect on

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multifunctionality types was significant and positive, meaning that specialized communities (low niche-skewness) were linked to low multifunctionality types. This relationship remained significant even when including vegetation cover and species richness, and the magnitude of its effect was similar or higher than that of cover (the second most influential predictor of multifunctionality types, Model 3, Table 7.1). In the model that exhibited highest statistical power (Model 4, Table 7.1), specialization was the main predictor and the interaction term with aridity was highly significant and positive (thus pointing to an increase in the effect of community specialization in the most arid sites).

Table 7.1. What drivers the existence of multifunctionality types?

Estimated coefficients of predictors of multifunctionality type following three generalized linear models. In Model 1 only spatial pattern was taken into account, in Model 2 specialization and aridity (plus their interaction) was included; in Model 3 total cover and richness were added and in Model 4 spatial pattern was removed from the analysis in order to increase statistical power. Null and residual deviance of the models are shown.

Predictors	Model 1	Model 2	Model 3	Model 4
Spatial pattern	1.08 ± 0.42 (*)	-0.08 ± 0.57 (n.s.)	-1.07 ± 0.7 (n.s.)	NA
Specialization	NA	1.22 ± 0.36 (**)	1.03 ± 0.4 (**)	1.12 ± 0.26 (***)
Aridity: Specialization	NA	-0.39 ± 0.31 (n.s.)	-0.3 ± 0.36 (n.s.)	0.93 ± 0.22 (***)
Aridity	NA	-0.72 ± 0.34 (.)	-0.47 ± 0.4 (n.s.)	-0.27 ± 0.25 (n.s.)
Cover	NA	NA	1.14 ± 0.41 (**)	0.55 ± 0.24 (*)
Richness	NA	NA	0.31 ± 0.3 (n.s.)	-0.01 ± 0.19 (n.s.)
Null Deviance	134.378	134.378	134.378	242.14
Residual Deviance	127.64	99.222	87.968	174.76

mean ± standard error

Signif. codes: n.s., not significant/ ., <0.1/ *,<0.5/ **,<0.01/ ***,<0.001"

Both community specialization and multifunctionality exhibited bimodal distributions and alternative states throughout the aridity gradient studied, which coexisted at aridity levels around 0.7-0.8 (Figure 7.2). Indeed, the association between the multifunctionality state and specialized communities (considered specialized if CW-Skewness < 0) was highly significant ($\chi^2 = 33.0$, $P \sim 10^{-8}$; when using Monte Carlo, $\chi^2 = 34.8$, $P \sim 5 \times 10^{-4}$) and by itself properly classified ~ 71% of our dataset (Figure 7.1).

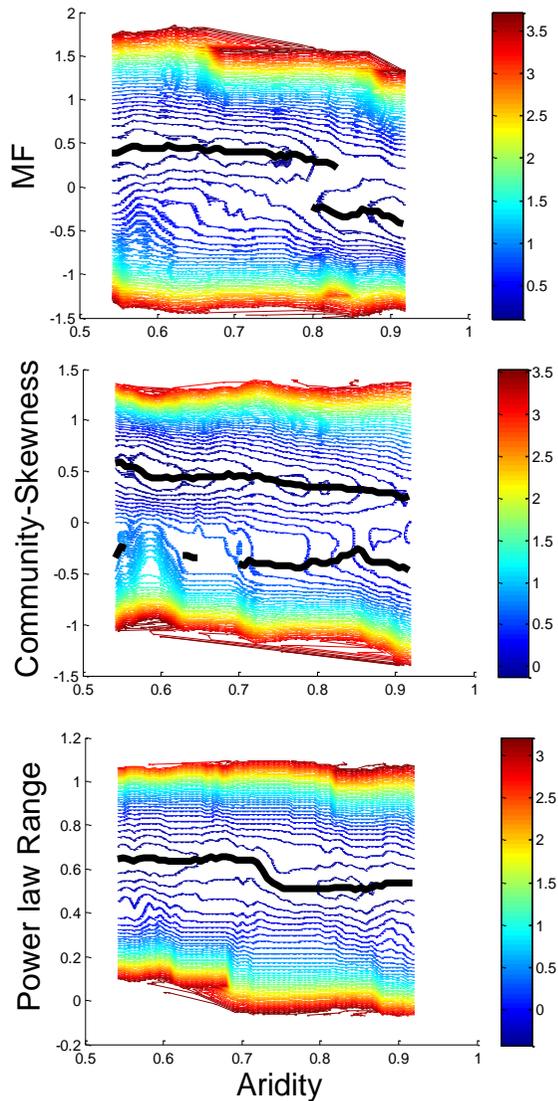


Figure 7.2. Alternative states of multifunctionality, community specialization and spatial pattern through aridity gradients.

Variation of the ‘stable’ states (i.e. local minima of the stability landscape; see Figure 7.1, black line) along the aridity gradient studied for multifunctionality (a), the Specialization (b) and power law relative range (c). Contour lines represent the estimated potential energy from which the ‘stable’ states are derived as local minima (as shown in Figure 7.1).

Trait syndromes associated to community specialization

Community specialization was negatively related with aridity and the CWM height (Table S 7.1). Importantly, the interaction between aridity and the effect of both CWM height and CWM SLA on community specialization was significant. At low aridity levels community specialization was positively related with CWM height and CWM SLA. In contrast, at high aridity levels community specialization was negatively related with CWM Height and CWM SLA (Figure 7.3). When the dataset was split per habitat type, grasslands did not show this interaction, which was maintained for shrublands (Figure S 7.2).

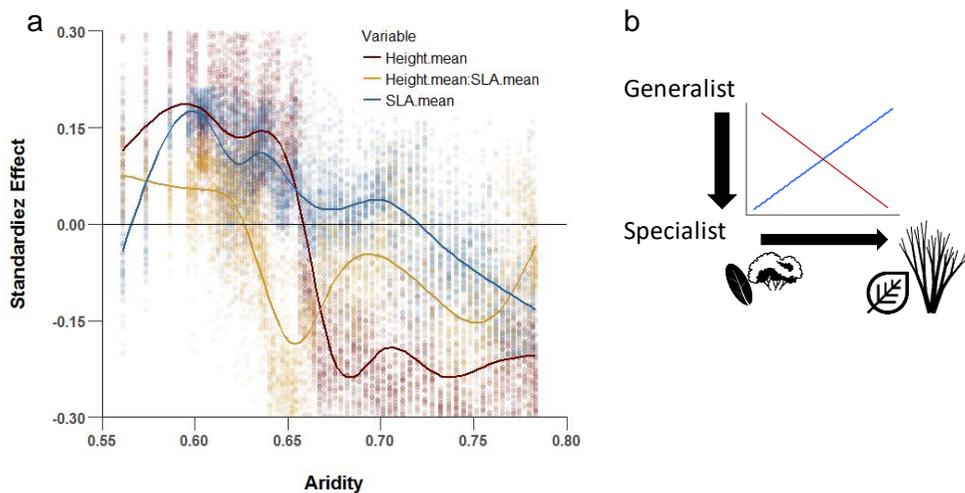


Figure 7.3. Shift in trait syndromes associated to community specialization through aridity gradients.

Effect of community weighted traits on explaining community specialization through an aridity gradient. a) Standardized effect sizes are displayed for Height mean, SLA mean and the interaction between both. This analysis is performed by fitting a generalized mixed model throughout a moving window that subsets our study sites following the gradient of community specialization. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects. b) Schematic representation of the relationships between CW-Skewness and traits. Red: negative standardized effect, Blue: positive standardized effect. Icons taken from noun project under creative commons license. Authors (left to right): Eccem Afacan; Laymik; Arthur Shlain; Richard Nixon.

Predictions on the expansion of specialized species

We identified 41 specialist species (Table S 6.2). These are mostly woody species (71%), with average height of around 170/59 cm, and SLA around 62.9/124.9 g/cm² for woody/grass species respectively. They belong to different families and their relative abundance vary substantially within our study sites.

We found that, with climate change, the distribution of specialist species was forecasted to expand of the current zones where they are living by ~60-200% depending on the scenario considered (assuming new colonization with habitat suitability increase of 0.6, see Figure S 7.3). Expansion areas include several zones all around the world, with substantial increases of habitat suitability in subtropical zones of Africa and South America and in many countries corresponding specially with zones that would become drylands with climate change (Huang et al. 2015) (Figure 7.4).

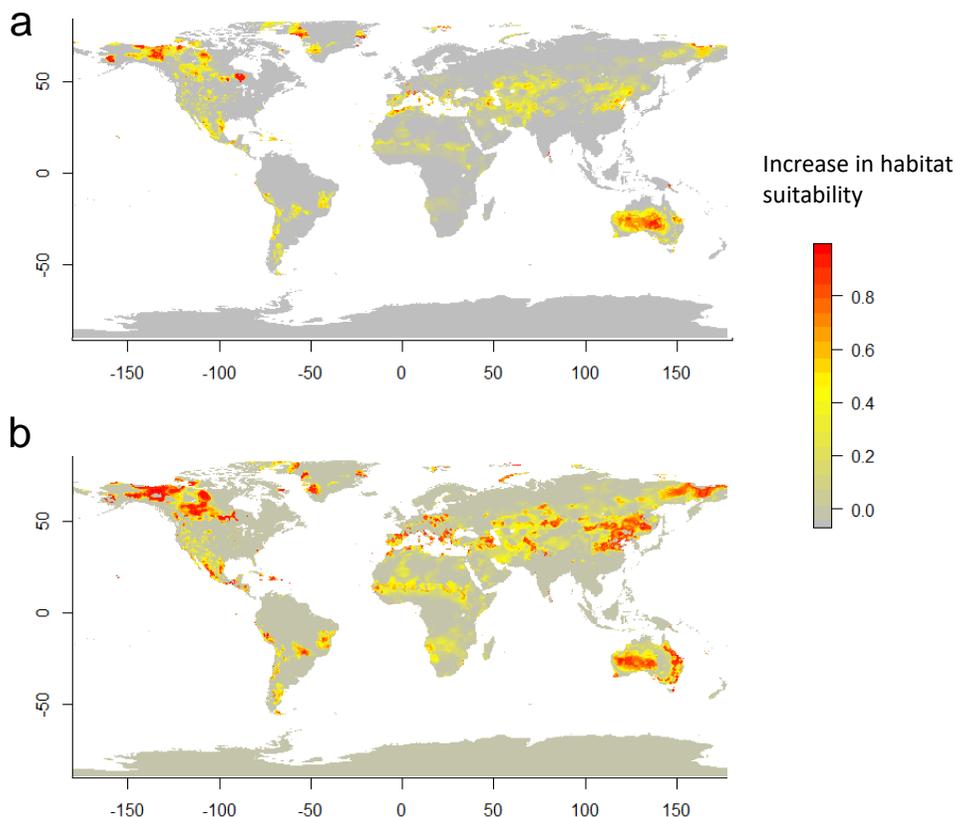


Figure 7.4. Specialists expansion with climate change

Vulnerable areas of the world to the expansion of specialists under different climate change scenarios. The maximum increase in habitat suitability of the 41 species identified in this work is displayed for RCP 4.5 (a) and RCP 8.5 (b) scenarios of climate change in 2100 according to Huang et al. (2015).

DISCUSSION

We uncovered a tight relationship between species specialization to aridity and multifunctionality that can explain why different plant spatial patterns are associated with each of the two multifunctionality types observed in global drylands (Berdugo et al. 2017). Our results demonstrate that the specialization process of communities is driven by a shift in the trait syndromes of species that can cope with aridity increments. In sites with aridity lower than 0.7, species adapt to arid conditions by decreasing their size and SLA, whereas in sites with aridity

higher than 0.7, the specialization of communities was linked to taller plants with higher SLA. The specialization of communities was strongly associated to the bimodal nature of multifunctionality. We found that climate change will increase the extent of zones where specialist species live by 60-200% by the end of this century, depending on the scenario considered, thus probably changing the average community specialization and producing losses of multifunctionality all over the globe.

Specialization drives the relationship between spatial pattern and multifunctionality states

Specialization was significantly correlated with the type of spatial pattern, with sites following a nonPL-like patterns being characterized by specialized communities. Specialization of communities has been found to be linked with facilitation-competition outcomes, specialist communities being driven by competitive interactions and communities that are not specialist by facilitation (Chapter 3). As spatial pattern is known to be driven by plant-plant interactions (Von Hardenberg et al. 2001, Manor and Shnerb 2008a, Meron 2015), we expected that specialization of communities (specialized if CW niche skewness was lower than zero) was impacting spatial patterns indirectly through the dominating type of plant-plant interaction in the community. PL-like patterns are driven by facilitative interactions (Kéfi et al. 2007b, Scanlon et al. 2007, Berdugo et al. 2017a) and in systems driven by competition isolated patches such as those seen in nonPL-like emerge (Von Hardenberg et al. 2001, Manor and Shnerb 2008a). Thus the results we found meet expectations, as PL-like and nonPL-like spatial patterns were associated with non-specialized and specialized communities, respectively ($\chi^2 = 10.93$, $P < 0.001$; when using Monte Carlo, $\chi^2 = 12.37$, $P < 0.001$). When specialization was included in the models, the effect of spatial pattern on multifunctionality became not significant (Table 6.1), thus suggesting that association between spatial pattern and multifunctionality is driven mainly by specialization. Although specialization can explain multifunctionality types better than spatial pattern, spatial pattern is still associated to multifunctionality types in ecosystems (Table 6.1), and this might be used to identify alternative states of multifunctionality when information about community composition is not available

(e.g., when using satellite or aerial images). Also, specialization was found to exhibit alternative states through aridity gradients (Figure 7.2). An important question is why plant spatial pattern is not showing alternative states despite being associated to both specialization and multifunctionality. In this regard, the fact that nonPL-like patterns might still occur in non specialized/high multifunctionality sites (Figure 7.2c) is worth further exploration, as an impediment on forming large plant patches might be a consequence of other factors that have not been taken into account in this study.

Our analysis shows that community specialization is the best indicator of multifunctionality types, even after accounting for plant cover, richness and aridity, which have been previously found to be important drivers of multifunctionality in drylands (Maestre et al. 2012a, Delgado-Baquerizo et al. 2013) (Table 6.1). Also, we found a significant interaction between community specialization and aridity, suggesting that the association between specialization and low multifunctionality is even higher at high aridity values. This interaction, together with the strong association between community specialization and multifunctionality states, suggest that specialist communities could be the main reason stabilizing low multifunctionality sites probably by exerting direct effects on nutrient cycling (de Bello et al. 2010, Mouillot et al. 2011, Valencia et al. 2015).

Community specialization summarizes information on both aridity and plant functional traits, which are known multifunctionality drivers (Lavorel and Garnier 2002, Delgado-Baquerizo et al. 2013, Valencia et al. 2015, Gross et al. 2017). This is likely the reason why aridity become a non-significant predictor of multifunctionality when specialization was added in the model. In previous works CW niche skewness was found to become negative (thus indicating that most of the community showed asymmetry for aridity preferences, i.e., specialization to arid conditions, Chapter 3) especially in high arid sites, thus being probably the reason underlying this interaction. The fact that specialization of communities is especially important for multifunctionality types in high arid sites highlights that specialized species exert probably differential controls on soil nutrients in these sites. This is also suggested by previous studies showing that, in low multifunctionality sites, soil nutrients driven by biotic processes (e.g. N) were especially limiting multifunctionality values (Berdugo et al. 2017a). This result also concurs with the results shown in Berdugo et al (Chapter 3), showing a shift in plant-plant

interactions and a change in the importance of biotic community assembly rules. Probably, the way in which plants impact soils affect directly the outcome of plant-plant interactions, as suggested in other studies (Maestre et al. 2002, 2003a, Padilla and Pugnaire 2006). In this regard, we hypothesize that plants contribution to soil nutrients might probably not be functional especially after aridity thresholds of 0.7. However, still processes such as environmental amelioration (through shading or water retention, i.e., abiotic amelioration *sensu* Wright *et al.*, 2017) might be playing a role, as suggested by the especial importance of facilitative processes shown in these aridity values for maladapted species (Chapter 3).

Shifts in trait syndromes explain specialization through aridity gradients

The analyses performed with functional traits showed that CW-Niche skewness showed contrasting relationships with functional traits depending on the aridity level in which the community occur. Whereas at low aridity communities with a higher degree of specialization are dominated by small species with low SLA (typically stress tolerants, *sensu* (Cornelissen et al. 2003), at high aridity communities are dominated by taller plants (~100 cm) with higher SLA (~ 60 g/cm², Figure 7.3), especially in shrublands (Figure S 7.2). This does not mean that at high aridity levels we always will find tall plants with high SLA, but that specialized communities in high aridity levels tend to have taller plants than the average species pool of high arid sites. This interaction is clarified by the fact that there is a shift in habitat types in the database from grassland to shrublands around aridity levels of 0.7. Still, shrublands exhibit a strong interaction between aridity and CWM Height when explaining specialization. Although high SLA and taller plants have been associated with high ecosystem functioning (e.g. Lavorel & Garnier 2002; Eldridge *et al.* 2011), some studies have found patterns such as ours suggesting a change in trait syndromes through aridity gradients (Gross et al. 2013, Le Bagousse-Pinguet et al. 2017b). Some studies state that plants increase water use efficiency either by reducing the size of their leaves (which produces low SLA with thick leaves, see Westoby *et al.* 2002; Wright *et al.* 2004) or by decreasing nitrogen content in the leaves (Poorter et al. 2009, Maire et al. 2015). These latter studies suggest that trait syndromes of tall plants and high SLA that are adapted to extremely arid conditions may correspond to stress avoidant shrubs (*sensu*, Chaves

et al. 2002). These plants use a strategy against aridity of producing low quality disposable leaves rapidly after rain pulses. To do so, plants exhibit high SLA values with low quality leaves (thus their production is not costly) to respond quickly to rainfall pulses (de Lillis and Fontanella 1992, Westoby *et al.* 2002, Wright *et al.* 2004, Poorter *et al.* 2009, Maire *et al.* 2015). Also, the risk of cavitation (the main reason why plants adapted to tolerate aridity are usually small, see Tyree & Sperry, 1988) in stress avoidant species is reduced by the fact that no leaves are produced in the driest moments of the year. Litter generated by these plants has been shown to usually have allelopathic compounds (e.g., *Artemisia herba-alba* (Escudero *et al.* 2000)) and are poor in nitrogen (Poorter *et al.* 2009, Maire *et al.* 2015), thus producing a negative impact on soil fertility (Valencia *et al.* 2015). Our results on the interaction of aridity and specialization to drive multifunctionality are reinforced by this change in syndromes, since multifunctionality might experience an important decrease if biotic inputs restrict to low nitrogen content leaves. Also, this is consistent with a decoupling between nitrogen and the rest of soil nutrients (mainly phosphorous) which has been found in previous studies in arid lands (Delgado-Baquerizo *et al.* 2013, Berdugo *et al.* 2017a), since this shift in trait syndromes would change importantly the amounts of nitrogen that are incorporated in the soil. Importantly this change in the strategy of species occurs at aridity values around 0.7 (Figure 7.3). Previous studies have suggested that around this same aridity levels ecosystems could not reach a stable equilibrium with the environment (non-equilibrium systems, see Vetter, 2005; von Wehrden *et al.*, 2012). This occurs because the variance in precipitation regimes makes vegetation extremely vulnerable to droughts and seasonal variations (Illius & O'connor 1999). In this context, changing adaptive strategy towards stress avoidance would be beneficial, as stress avoidant species would likely be more plastic and resistant to this natural stochasticity of climate.

Can we use specialization to predict shifts in multifunctionality states with climate change?

The strong association found between community specialization and multifunctionality types suggests that the former might be used itself as a marker of multifunctionality types. Specialization was not only found to be associated to

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multifunctionality types, but also was found to exhibit bimodal patterns of variation with aridity. There is no study aimed at the suitability of using community shifts towards specialists as early warning signals of tipping points such as the one suggested by the bimodal pattern of multifunctionality in our study. As specialization of the community is a weighted mean of specialization of individuals within the community, we argue that tracking abundance of some individuals known to be specialist in a community may be used as early warning signals of shifts in multifunctionality. Because the link we found between community specialization is correlational, we cannot provide evidences on whether the system will experience drastic losses of functioning after or before community specialization. However, the association between community composition and multifunctionality has been proven experimentally to happen directionally from community composition to soil characteristics (Mouillot et al. 2011, Valencia et al. 2015), thus community shifts should precede multifunctionality losses. Therefore, the early detection of specialists over-dominance might indicate that the system is changing or is going to change, probably associated with sharp decreases in ecosystem functioning. Those changes in dominance occur slowly, thus focusing on seedling monitoring is probably the way of spotting these changes in advance.

Of course, under no circumstances our study should be taken as a motivation to eradicate specialist species in arid drylands. First, because these species are the only ones able to cope with very high aridity levels, and therefore their extinction in these areas would irrevocably foster the degradation of these zones. Second, because until the exact mechanisms of the link between specialization and multifunctionality types are fully understood, we cannot claim that specialists are causing those shifts, thus their suitability as indicators might be misleading. Third, specialists have been found to facilitate preferentially maladapted species in arid lands (Chapter 3), thus their eradication might extinguish the only chance of the latter of surviving climate change. Also, future studies should get more insights into the association between specialist communities and multifunctionality using dynamical data, since the inclusion of new species into a community might concur with changes in the dynamical behaviour of the system (e.g., increasing competition importance see Chapter 3) that makes the output of this process rather uncertain.

Predicting shifts in habitat suitability of specialists with climate change

As species expansion with climate change may be estimated using species distribution models (see (Elith and Leathwick 2009), we were able to forecast the possible response of some specialist species to aridity increments (Figure 7.4). By using species distribution models to interpolate the niches of species into aridity scenarios of climate change, we found that, with climate change, the distribution of these species was likely to expand of their current zones by ~60-200% depending on the scenario considered. We located some areas in which these increments are specially high such as in subtropical zones of Africa and South America and in many sites corresponding with zones that would become drylands with climate change (Huang et al. 2015) (Figure 7.4). It must be noted that: i) our study did not include any species belonging to Indo-malasian ecozones, therefore no predictions could be done in this area, and ii) many more specialist species than those evaluated here may occur in Asia and Africa, where only a few sites could be studied. We identified five main sources of specialist species according to our database: central-west of North America, south-west of South America, Australia, northern west coast of Africa and East coasts of Mediterranean Sea (Figure S 7.4). Because the association between specialization and multifunctionality occurs at the community level, we cannot prove that increases in habitat suitability of species might entail shifts in multifunctionality. However, our results are the first pointing to potential areas where this might happen only by tracking distributional shifts of species. We argue that, if specialization occurs at the community level, our results predict that 70% of these areas becoming specialized (CW niche skewness shift into negative values) will likely experience drastic declines on multifunctionality.

CONCLUDING REMARKS

Forecasted increases in aridity with climate change will change the composition of dryland plant communities, making them more dominated by specialists to more arid conditions. Our findings indicate that this change might entail sharp decreases in multifunctionality, which are also linked to shifts in the spatial pattern of vegetation. We were also able to link specialization of communities with a shift in the strategies of species to cope with abiotic stress (from stress-resistant to stress avoidant), thus uncovering potential mechanisms by which specialization may

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impact multifunctionality. Our results contribute to our understanding of why multifunctionality exhibits two states across drylands and suggest that over-dominance of specialist species (which occur gradually and therefore might be spotted in advance) might be used as an early warning signal of changes in multifunctionality associated to climate change if those are demonstrated to be the reason causing abrupt shifts in multifunctionality. By finding a tight relationship between community specialization, and multifunctionality states, we were also able to extrapolate how specialist species will increase their habitat suitability in the future, thus being able to suggest potential areas where multifunctionality shifts may occur with climate change. Future studies need to investigate whether specialists are the main cause of these shifts, and whether their increase in dominance is dynamically predictable in areas where they were not currently found. By disentangling the links between community specialization, multifunctionality stable states and spatial pattern of vegetation, our study provide key insights to understand the mechanisms behind the alternative states of multifunctionality observed in dryland ecosystems, and provide forecasts that can be used to improve the management of dryland communities.

SUPPLEMENTARY TABLES**Table S 6.1. Relationship between traits and community specialization**

Standardized effect sizes of the generalized lineal models performed using as response variable CWM skewness. Abrev.: CWM: community weighted mean, SLA: specific leaf area.

Variable	Effect
CWM (Height)	-0.37 ± 0.10 ***
CWM (SLA)	-0.08 ± 0.07 (n.s.)
Aridity	-0.86 ± 0.07 ***
CWM(Height) X CWM(SLA)	0.02 ± 0.08 (n.s.)
CWM(Height) X Aridity	-0.69 ± 0.12 ***
CWM(SLA) X Aridity	-0.35 ± 0.09 ***
CWM(Height) X CWM(SLA) X Aridity	-0.56 ± 0.11 ***
Ajusted R ²	0.62
F-statistic (7,108)	27.5

mean \pm standard error

Signif. Codes: n.s.: not significant; *** <0.0001

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Table S 6.2. Dryland specialists list

List of specialists (CW-Skewness < 0) found in this study with at least 10% of average relative cover through sites. Ab: mean of relative abundance, Op: species niche optimum, mAb: minimum of relative abundance, MAb: Maximum of relative abundance, N: number of sites in which species is found in the dataset.

Species	Ab	Op	mAb	MAb	N
<i>Festuca orthophylla</i>	66.13	1.00	21.26	99.65	11
<i>Casuarina pauper</i>	57.33	0.87	57.33	57.33	1
<i>Festuca pallescens</i>	54.71	0.83	30.33	79.10	2
<i>Coleogyne ramosissima</i>	49.41	0.86	13.20	71.45	4
<i>Flourensia cernua</i>	47.65	0.82	39.46	55.84	2
<i>Noaea mucronata</i>	46.29	0.90	8.11	95.55	10
<i>Baccharis linearis</i>	44.66	0.93	8.74	80.58	2
<i>Larrea cuneifolia</i>	34.73	0.89	1.22	64.03	5
<i>Eremophila mitchellii</i>	34.21	0.66	20.86	53.24	5
<i>Ambrosia dumosa</i>	30.37	1.00	7.42	54.85	6
<i>Artemisia filifolia</i>	29.59	0.85	29.59	29.59	1
<i>Larrea tridentate</i>	25.56	1.00	5.62	77.47	18
<i>Eremophila sturtii</i>	24.81	0.87	0.12	57.36	3
<i>Bahia ambrosioides</i>	22.31	1.00	11.73	43.09	3
<i>Tetracoccus fasciculatus</i>	21.45	0.92	9.62	47.32	6
<i>Stipa speciosa</i>	21.07	0.85	13.66	32.11	6
<i>Myoporum platycarpum</i>	20.52	0.82	3.63	32.91	4
<i>Geijera parviflora</i>	17.42	0.68	15.19	20.11	3
<i>Opuntia streptacantha</i>	17.23	0.73	17.23	17.23	1
<i>Festuca argentina</i>	16.74	0.84	14.17	18.63	3
<i>Lepidium leptopetalum</i>	16.05	0.83	16.05	16.05	1
<i>Stipa nardoides</i>	15.84	1.00	15.84	15.84	1

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<i>Hammada scoparia</i>	15.21	0.89	0.70	29.72	2
<i>Nassauvia glomerulosa</i>	15.15	0.84	2.40	40.04	3
<i>Ericameria nauseosa</i>	14.82	0.77	1.39	44.75	5
<i>Atriplex canescens</i>	14.54	0.96	0.46	44.49	4
<i>Tetraglochin alatum</i>	14.08	0.86	0.69	45.79	4
<i>Alectryon oleifolius</i>	13.96	0.86	0.06	49.34	7
<i>Mulinum spinosum</i>	13.94	0.85	0.75	30.49	4
<i>Rhus tripartite</i>	13.75	0.92	13.75	13.75	1
<i>Parastrephia quadrangularis</i>	13.34	1.00	1.54	34.10	6
<i>Ephedra torreyana</i>	13.13	0.83	1.73	25.11	3
<i>Stipa tenuis</i>	13.07	0.84	0.25	28.75	4
<i>Sporobolus contractus</i>	12.96	0.84	12.96	12.96	1
<i>Enteropogon acicularis</i>	11.13	0.68	0.55	47.88	5
<i>Pituranthos tortuosus</i>	10.97	0.97	2.90	20.00	3
<i>Bougainvillea spinosa</i>	10.50	0.90	10.50	10.50	1
<i>Acacia colletioides</i>	10.48	0.80	0.32	32.22	7
<i>Ephedra viridis</i>	10.24	0.84	10.24	10.24	1
<i>Dalea bicolor</i>	10.18	0.77	10.18	10.18	1
<i>Cylindropuntia leptocaulis</i>	10.03	0.80	2.62	27.96	4

SUPPLEMENTARY FIGURES

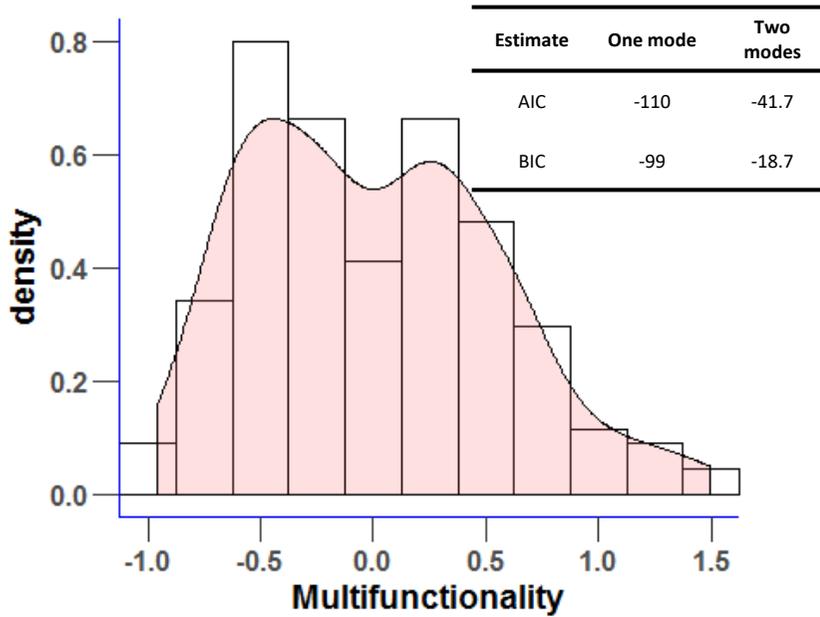


Figure S 7.1. Bimodality in multifunctionality

Histogram of multifunctionality and density estimation of the plots used in this study. Adjacent table shows akaike and Bayesian information criterion values (AIC/BIC respectively) for the Gaussian mixture fitting of one mode and two modes. Higher (less negative) values indicate most plausible models.

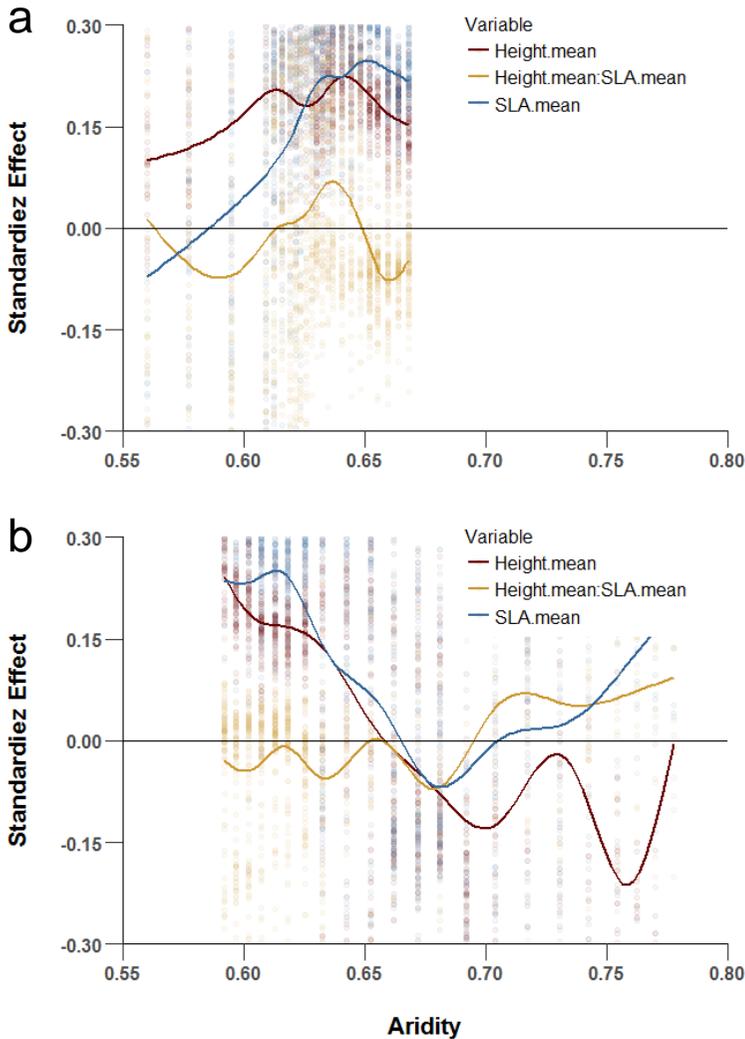


Figure S 7.2. Insights of the effect of habitat type on trait syndromes shift as predictors of community specialization through aridity gradients

Effect of community weighted traits on explaining community specialization through an aridity gradient for grassland sites ($N = 55$, a) and shrubland sites ($N = 61$, b). Standardized effect sizes are displayed for Height mean, SLA mean and the interaction between both. This analysis is performed by fitting a generalized mixed model throughout a moving window that subsets our study sites following the gradient of community specialization. Bootstrapped coefficients of this regression within the 95% confidence intervals are displayed for each step of the moving window. Lines are the gam smoothed trend of variation of the effects.

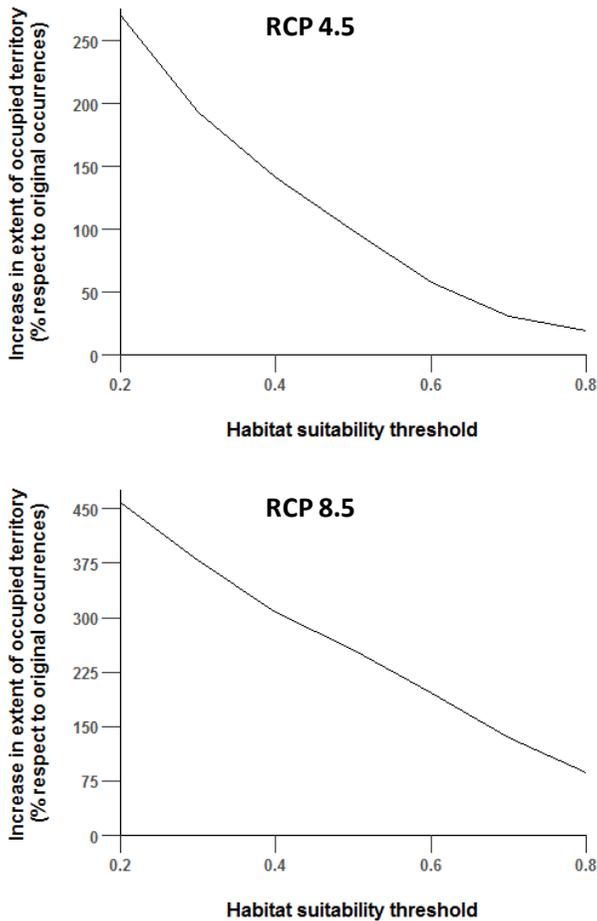


Figure S 7.3. Increase in extent related to habitat suitability threshold for new colonization

Increase in the extent of specialists occupied zones respect to the current extent of occupied zones as a function of several thresholds in habitat suitability for Representative concentration pathways 4.5 and 8.5. The thresholds indicate points from which habitat suitability increase would be sufficient to allow specialists recruitment in a new zone.

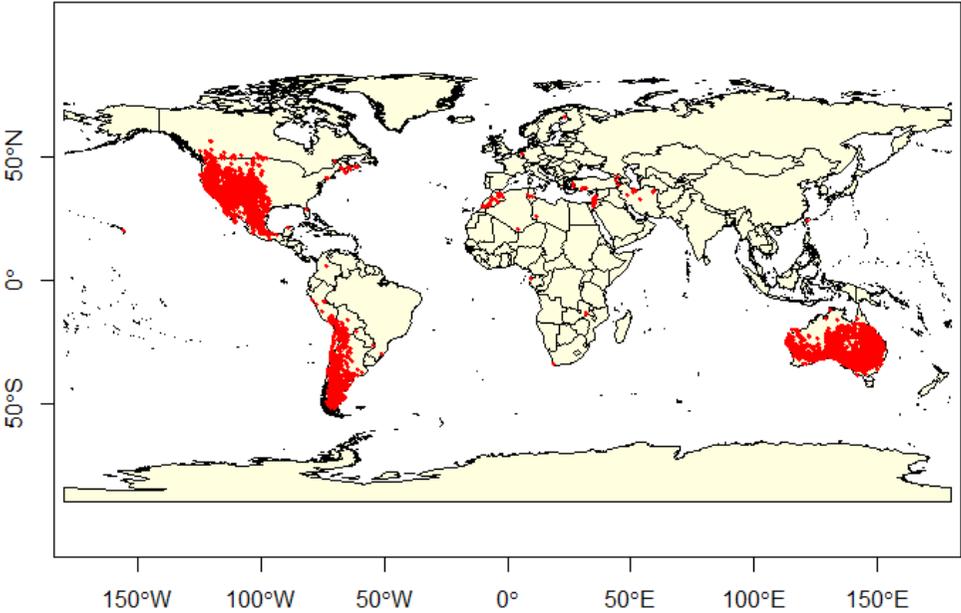
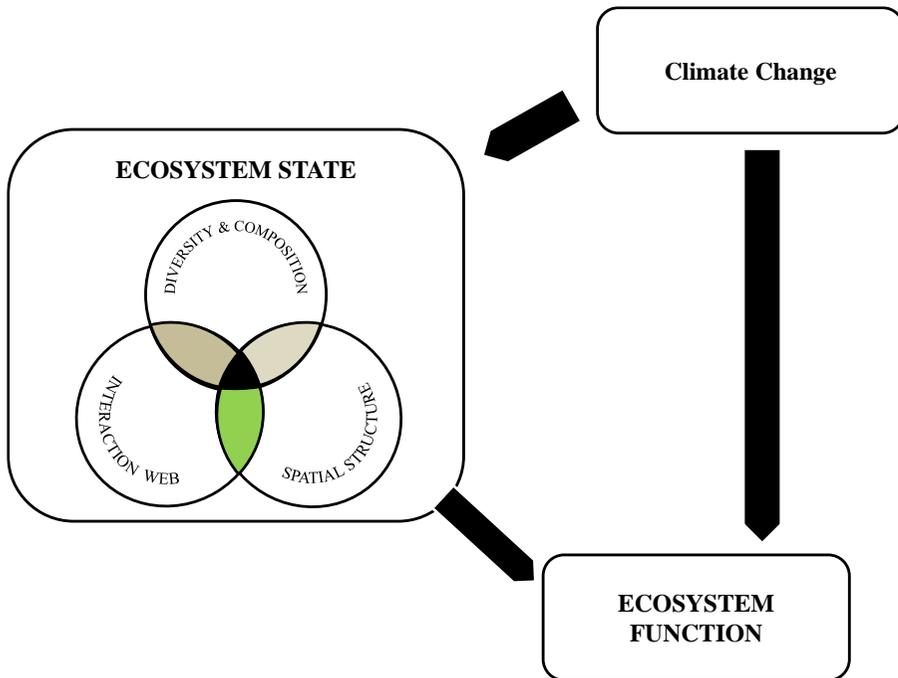


Figure S 7.4. Focal points of expansion of specialists
Current location where specialists are found, thus indicating possible expansion areas.

DISCUSSION

Aridity threshold involving ecosystem functioning, community structure, spatial pattern and plant-plant interactions uncovered.



Discussion

A THRESHOLD AT ARIDITY LEVELS OF 0.7 PROMOTES CHANGES IN ECOSYSTEM STRUCTURE AND FUNCTIONING IN GLOBAL DRYLANDS

Aridity is predicted to increase throughout the globe in the next century (Huang et al. 2015). As drylands are likely to experience nonlinear changes in response to these aridity increments (Ogle and Reynolds 2004, Bestelmeyer 2006, Delgado-Baquerizo et al. 2013, Luo et al. 2017), the relevance of studying thresholds in structural and functional attributes of their ecosystems has been stressed (Bestelmeyer 2006, Groffman et al. 2006). However, studies studying nonlinear changes in ecosystems with climate change have so far mainly been theoretical (e.g., Rietkerk *et al.* 2004; Briske *et al.* 2006; Kéfi *et al.* 2007a; Smith *et al.* 2009) and, in cases where empirical approaches have been conducted, their spatial extent has not been sufficient to generalize the patterns found (e.g., Maestre & Escudero 2009; Bestelmeyer *et al.* 2013). This thesis aimed at filling this gap of knowledge by using a global survey of dryland ecosystems (Maestre et al. 2012a).

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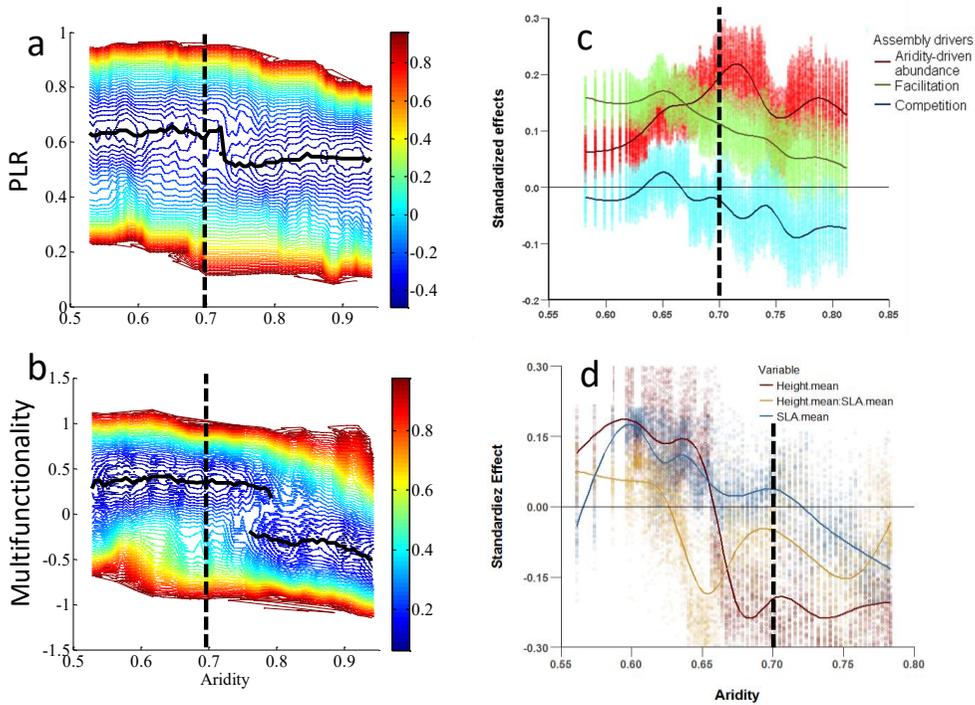


Figure 8.1. Aridity thresholds in global dryland ecosystem components.

Thresholds found in the different components studied (a, spatial pattern, as power law range, see chapter 2; b, multifunctionality, see chapter 2; c) importance of assembly drivers, see chapter 3; d) drivers of community specialization, see chapter 4). Note that scales in aridity are different; dotted lines represent Aridity values of 0.7.

We identified a clear threshold behaviour of global dryland ecosystems at aridity values (1-Aridity Index) around 0.7 (Figure 8.1). These aridity values are similar to those separating between semi-arid and arid regions of the world (Aridity \sim 0.8). This separation was first proposed by the UNESCO and is based on the suitability of drylands to sustain agricultural practices without irrigation (which is possible in semiarid areas but not in arid areas, see Middleton & Thomas, 1992). However, there is little information about ecosystem responses around this threshold. We found that, at this aridity level, several aspects of ecosystem structure and functioning changed qualitatively and quantitatively, sometimes in abrupt ways. By investigating the relationships between multiple structural attributes and

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multifunctionality we were also able to identify possible drivers of this threshold (Figure 8.2), which are discussed below.

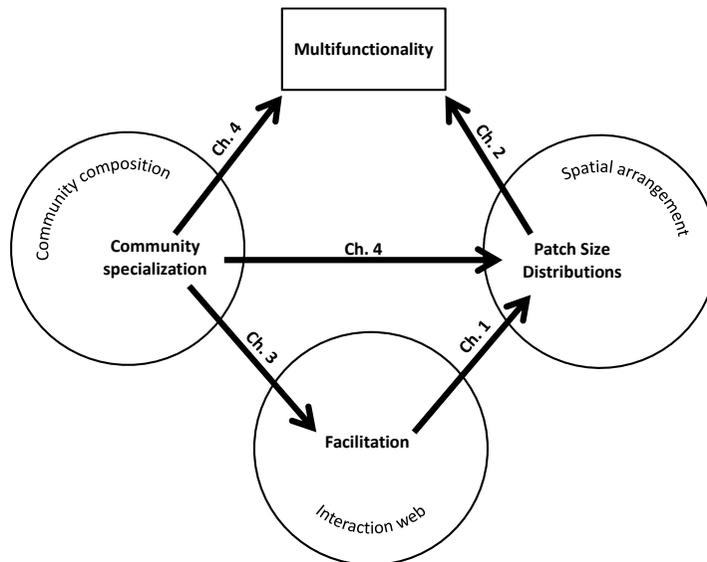


Figure 8.2. Summary of ecosystem components studied in this thesis.

Diagram showing the components studied and their relationships. Chapters in which the different links were studied are pointed in the arrows.

Spatial patterns may indicate thresholds in ecosystem functioning

Plant spatial patterns have been studied in drylands in conjunction with the occurrence of thresholds (e.g., Rietkerk *et al.* 2004; Kéfi *et al.* 2007a, b, 2010b). This occurs because the spatial pattern of vegetation is known to respond to hysteretic thresholds in models (Kéfi *et al.* 2007a, Scheffer *et al.* 2009) and because the formation of spatial patterns in nature is linked to complexity theory since its early days (Meron 2015). Indeed, the role of spatial patterns as indicators of abrupt changes in the functional status of the ecosystem has been discussed in the last decade. Kéfi *et al.* (2007) suggested that patch size distribution (a metric of spatial pattern of vegetation) could indicate the onset of desertification. While some field studies have shown the role of the spatial pattern of the vegetation on ecosystem functioning by preventing soil erosion, increasing water infiltration rates and increasing nitrogen mineralization rates (Aguiar and Sala 1999, Bautista *et al.*

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2007, Pueyo et al. 2012) other studies however have observed that cover is a better predictor of ecosystem functioning than spatial pattern in drylands (Maestre and Escudero 2009, Bestelmeyer et al. 2013). These contrasting findings started a debate on whether the plant spatial pattern may provide different information than total cover regarding ecosystem functioning (Maestre and Escudero 2009, Kéfi et al. 2010a, Bestelmeyer et al. 2013, Zurlini et al. 2014).

In this thesis, we found that total cover explains ecosystem multifunctionality better than patch size distributions across dryland ecosystems worldwide. However, we found that changes in ecosystem multifunctionality are not necessarily linear, as they present two stable types (high and low, driven by changes in soil fertility). These two types of ecosystem functioning were only predicted by patch-size distributions, with particularly strong associations between spatial pattern and multifunctionality at aridity values between 0.6 and 0.8 (where the two stable multifunctionality types co-occur). In this regard, we found two types of spatial patterns that changed abruptly at these aridity values. The first type, characterised by large patches producing power law-like (PL-like) patch-size distributions, is associated with high multifunctionality sites. The second type corresponds to curved patch-size distributions (non PL-like) and is linked to low multifunctionality sites. Thus, we argue that, although cover is a better multifunctionality predictor than spatial pattern, the bimodal nature of multifunctionality observed in our global dataset can only be explained by patch size distributions. Whereas in high multifunctionality sites both biotically- (carbon and nitrogen) and abiotically-controlled (phosphorous) nutrients drive multifunctionality, the latter is driven solely by biotically-controlled nutrients in low multifunctionality sites, suggesting low biological inputs (e.g., litter amount and decomposition) in these ecosystems. Other studies have already found a decoupling of C and P (Delgado-Baquerizo et al. 2013), or changes in nitrogen turnover rates (Wang et al. 2014) at aridity values of 0.7-0.8 in global and Chinese drylands, respectively.

Spatial patterns are driven by different drivers depending on their type

We found that each of the patch-size distribution types found is driven by different factors, thus suggesting an important change in the ecosystem dynamics associated to each spatial pattern. In sites with PL-like patch-size distributions (PL-like sites),

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aridity and total plant cover were linked, whereas they were not in sites with non PL-like patch-size distributions (non PL-like sites). The latter findings suggests that factors other than climate might be driving the functioning of non PL-like sites. Cover was also a main driver of PL-like sites, and aridity directly controlled patch size distributions in non PL-like sites. The links observed between total cover and patch-size distributions in PL-like sites is correlational, and this prevents us from establishing cause-effect relationships. In other words, we could not test whether PL-like patterns increase the total cover of the system (e.g., via facilitative interactions occurring in large plant patches, see Maestre & Cortina 2005), whether in ecosystems with high total cover clumps of vegetation appear because of the lack of space (thus patch-size distributions look more PL-like). Spatial patterns and their formation through facilitative mechanisms have been theoretically linked with a higher biomass than it would be expected solely by climatic conditions (Noy-Meir 1973, Aguiar and Sala 1999, Puigdefabregas et al. 1999a, Boer and Puigdefábregas 2005b, Kéfi et al. 2007b, Xu et al. 2015b). This has been invoked as a major mechanism creating hysteretic thresholds on total cover of ecosystems in models (Kéfi et al. 2007b, 2016, Xu et al. 2015b). However, we did not find a clear threshold in total cover, which decreased linearly with aridity regardless of the spatial pattern exhibited. In this regard, it is important to note that neither spatial patterns nor total cover are accounting for the cover of small beneficiary species observed at our study sites (not distinguishable at the scale of spatial patterns, and not included in the total cover survey if they were already under the canopy of their nurses). Indeed, we found that facilitation did exert an increase in the abundance of these rare species in Chapter 3, but this was not reflected in the overall vegetation cover. Some studies have also found shifts in the relative importance of aeolian vs hydrologically driven sediment depositions between semi-arid and arid ecosystems (Ravi et al. 2007), which are thought to play an important role in the formation of plant spatial patterns (Ravi et al. 2008) and that suggest a shift in the abiotic drivers of patch formation through aridity gradients around the threshold we found. This has not been studied in this thesis, and future studies should investigate the interaction of soil erosion as spatial pattern drivers and their interaction with the ones we found.

Most importantly, in Chapter 1, we found a clear relationship between facilitation and PL-like spatial patterns, thus linking the emergence of these patch size distributions to the higher frequency of facilitative interactions. Such a link has

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been hypothesized multiple times by modelling studies (Von Hardenberg *et al.* 2001; Kéfi *et al.* 2007b, 2010b) but our results provide, to the best of our knowledge, the first empirical evidence of the association between positive plant interactions and PL-like spatial patterns. Moreover, when we investigated the relative importance of facilitation as an assembly driver in Chapter 3, we found that facilitative interactions at the community level collapse at the same aridity level as patch size distributions shift from PL-like to non PL-like. I argue that communities driven by competition would result in spatial patterns characterised by isolated individuals, which explains also why non PL-like patterns described in Chapter 1 were driven by the community weighted mean of plant height, as previously suggested (Manor & Shnerb 2008; Xu *et al.* 2015), whereas communities driven by facilitative interactions will likely create larger patches merging different species and individuals (thus looking like PL-like distributions, see Kéfi *et al.* 2007b; Scanlon *et al.* 2007; Manor & Shnerb 2008b).

Does facilitation affect ecosystem functioning through patch formation?

The role of facilitation for enhancing ecosystem functioning has been often hypothesized (Brooker *et al.* 2008), but empirical studies have failed to demonstrate it empirically (Mitchell *et al.* 2009, Maestre *et al.* 2010). The main mechanism invoked to link facilitation and ecosystem functioning is the positive link between facilitation and species richness/diversity within communities (Verdú and Valiente-Banuet 2008, Cavieres and Badano 2009, Soliveres *et al.* 2015a), which would enhance ecosystem functioning via niche complementarity (Tilman *et al.* 1997). There is, however, an alternative framework to explain relationships between ecosystem functioning and biodiversity, which relies more on the effect that dominant species exert on ecosystem functioning (the mass ratio hypothesis, Grime 1998). It is possible to transfer this hypothesis to facilitation by linking patch formation and facilitation, which is directly related to the role of species best adapted to local conditions on acting as nurses (Valiente-Banuet *et al.* 2006, Soliveres *et al.* 2015a). Indeed, the results of Chapter 3 suggest that the role of facilitation as an assembly driver, together with the importance of this driver to create clumps of vegetation in spatial patterns (Chapter 1), may influence the ability of ecosystems to maintain high multifunctionality levels. This finding points to a mechanism driving the relationship between facilitation and ecosystem functioning more related to the mass-ratio framework and to the role as resources

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sink that large vegetation patches play in drylands (Aguiar and Sala 1999), than to the complementarity framework (Tilman et al. 1997). In other words, our results suggest that the impact of facilitation on ecosystem functioning may be caused more by promoting the creation of larger patches (Chapter 2) than by its effects on maintaining species richness. Our findings indicate that facilitation would impact ecosystem functioning by promoting large plant patches up to a threshold value of 0.7 (where it is a dominant assembly driver of communities and drives PL-like spatial patterns). However, even in communities whose assembly is mainly driven by competition, we also found that facilitation is still important to maintain the abundance of those species that are not adapted to the environmental conditions of the sites they inhabit. In this regard, a reliable hypothesis is that facilitation might exert different effects on ecosystem functioning depending on the degree of aridity. Whereas in sites with aridity values lower than 0.7 facilitation plays an important role as a driver of community assembly (Chapter 3) and in the creation of plant patches (Chapter 1), in sites with higher aridity levels facilitation could still play a role in preserving maladapted species (see Chapter 3), thus exerting its effect on ecosystem functioning through the complementarity mechanism. Moreover, recent studies (Gross et al. 2017) showed that communities tend to maximize their functional diversity, maximizing ecosystem functioning at the same time. Because facilitation might play a role in this process (as suggested in Chapter 3 by the high importance of facilitative interactions as an assembly driver), future studies should investigate the ability of facilitation to assemble functionally-optimized communities (i.e., as functionally diverse as possible given the abiotic conditions, see Gross *et al.* 2017) rather than looking at the overall performance of ecosystem functioning. In this regard, facilitation has been shown to increase functional trait spectrum of the community (Butterfield and Briggs 2011, Schöb et al. 2012) specifically by promoting species with different traits than the nurses (Valiente-Banuet and Verdú 2007, Soliveres et al. 2014a, Schöb et al. 2014).

Changes in species composition drive the importance of facilitation as an assembly driver

The importance of facilitative interactions between plants across environmental gradients is an important topic in community ecology that has involved different hypotheses and controversies (Bertness and Callaway 1994, Michalet et al. 2006, Brooker et al. 2008, Holmgren and Scheffer 2010, Soliveres et al. 2012, Soliveres

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and Maestre 2014). The main hypotheses proposed so far argue that facilitative interactions may increase with increasing abiotic stress (Callaway et al. 2002, Callaway 2007), show a humped-shape along gradients of increasing environmental harshness (Michalet et al. 2006, Holmgren and Scheffer 2010) or depend on species-specific adaptations (Choler et al. 2001, Greiner La Peyre et al. 2001, Liancourt et al. 2005). Typically, most previous studies on facilitation have focused on particular nurse-beneficiary pairs, which produces different results than looking at all possible combinations of pairs in the community (Cavieres et al. 2006, Cavieres and Badano 2009). In this thesis, by examining all species pairs of the communities in drylands worldwide and by specifically accounting for species-specific adaptations, we showed that the importance of facilitation as an assembly driver decreased at high aridity levels, waning at aridity levels around 0.7. This threshold also corresponds to a higher degree of species specialization to aridity, suggesting a tight relationship between species-specific adaptations and the outcome of plant-plant interactions, thus strongly supporting the last of the three hypothesis (i.e., that species characteristics determine the outcome of facilitation importance more than stress, Soliveres *et al.* 2012, 2015; Soliveres & Maestre 2014), and shows emerging patterns supporting hump-shaped trends in the importance of facilitation through aridity stress. Interestingly, other studies did not find this relationship in global gradients for facilitation-richness relationships (Soliveres and Maestre 2014), where they found monotonical increase of species richness throughout all aridity gradient studied. This suggest that the role of facilitation on increasing recruitment of perennial species might be different than the role it exerts on the relative abundance of species (more related with growth of species). In this regard, our results suggest that nurses might be unable to promote growth of other perennials given a critical resource shortage (reached in our case at aridity values of 0.7). Specifically, we conclude that communities dominated by specialists are more likely to assemble through competition, whereas communities in which specialists do not dominate are driven by facilitation. Importantly, facilitation might exhibit an important function on the most maladapted species in specialist-dominated communities. The mechanism by which this happens is probably related to the fact that maladapted species need a minimum environmental amelioration to thrive in these environments (Liancourt et al. 2005, Soliveres et al. 2015a). On the other hand, adapted species can thrive by themselves and therefore facilitation does not outweigh competition, which intensity is probably increasing with environmental stress due to resource shortages (Welden and Slauson 1986).

Compositional shifts and their impact on spatial patterns and multifunctionality

We found a progressive specialization of the species pool with increasing aridity. In particular, the species niches in dryland communities showed a marked trend toward being right-skewed (i.e., specialized to more arid conditions) around aridity thresholds of 0.7. Studies at global scales using this same database have shown changes in beta diversity at similar values (around 0.8, see Ulrich *et al.* 2014), as well as important changes in functional composition of communities around these aridity values in the sites we surveyed along a regional gradient in Spain (Gross *et al.* 2013). This thesis has made three important advances on our understanding of the consequences of species turnover towards communities specialized to aridity:

- i) The specialization of the community affects plant spatial patterns by influencing the relative importance of plant-plant interactions. I introduced in Chapter 4 a link between community composition and plant spatial patterns that was virtually missing in the literature, except for some studies focused on the formation of patches of particular functional types such as shrubs or grasses forming tussocks (Lett and Knapp 2003, Ravi *et al.* 2007). These studies found a relationship between these functional types and vegetation patterns mainly due to the way in which these functional types grow (e.g., pattern created due to clonal reproduction), but never investigated the specialization of species as a driver of pattern formation. The results presented in chapter 3 suggest that communities dominated by species specialized to aridity will likely not create large plant patches, a result that was confirmed in Chapter 4.
- ii) The results of Chapter 4 suggest that the relationship between functional traits and community specialization interacts importantly with aridity, meaning that the ability of species to cope with environmental stress is related to different trait syndromes depending on whether the aridity of the site is above or below this threshold. This suggests a change in the strategy of species from stress tolerant to stress avoidant around an aridity value of 0.7. This shift in trait composition has already been suggested in the literature

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(Gross et al. 2013), but this thesis links it clearly to the specialization of the aridity niches at global scales, thus helping elucidating some of the mechanisms underlying this shift in trait syndromes. One of them could be related to uncertainty in precipitation regimes. It has been hypothesized that coefficients of variation of precipitation regimes of around 33% imply a threshold value that shifts the type of ecosystem dynamics from equilibrium to non-equilibrium ecosystems (Ellis and Swift 1988). Whereas equilibrium ecosystems are assumed to have reached a steady state in relation to their climate, in non-equilibrium systems uncertainty in precipitation patterns preventing the community to reach an equilibrium (Ellis and Swift 1988). This threshold has been suggested to happen between arid and semiarid regions, thus changing the dynamical behaviour of ecosystems into a more non-equilibrium regime in arid regions (Sullivan and Rohde 2002, von Wehrden et al. 2012a). The change in the strategy of species to stress avoidant syndromes observed in this thesis would fit this change in the dynamics of climate, as stress avoidant species are more plastic to cope with the characteristic uncertainty of precipitation regimes in non-equilibrium regimes.

- iii) I found an important link between community specialization and ecosystem functioning that linked the bimodal patterns of multifunctionality with communities specialized to aridity. I hypothesize that the specialization of communities promotes lower N content and less decomposability in the leaves (Poorter et al. 2009, Maire et al. 2015), which eventually reduce soil fertility and ecosystem functioning. Importantly, because the shift in community composition identified in Chapter 4 is directly linked to the ability of species to thrive in arid conditions, it is possible to forecast its occurrence with climate change. The tight dependence between shifts in community composition and variations in the relative importance of facilitation/competition, plant spatial patterns and multifunctionality suggests that we could use these shifts to forecast fundamental changes in ecosystem properties and functioning under climate change, as we discuss in the next section.

IMPLICATIONS WITH CLIMATE CHANGE

This thesis identified a threshold value on aridity ~ 0.7 in which several aspects of ecosystem attributes, dynamics and functioning change abruptly. Using a space by time substitution it is possible to evaluate how global warming will force different areas of the world to cross this threshold in near future. I used aridity forecasts provided by Huang *et al.* (2015) to make an educated guess about zones of the globe that might suffer discontinuous transitions such as the ones shown in this thesis (involving community specialization, multifunctionality abrupt losses and waning of facilitation importance as an assembly driver, spotted in this thesis at aridity levels of 0.7) with increasing aridity (Figure 8.3). Huang *et al.* (2015) developed the most updated forecast of aridity increments in the next century for the globe under two contrasted scenarios of climate change (Representative Concentration Pathways 8.5 and 4.5, inferring exponential and saturated increases of CO₂ emissions respectively, see Stocker *et al.* 2013). By inferring that changes in ecosystem may occur abruptly when crossing aridity ~ 0.7 (as suggested in this thesis), the results show that up to 11% of emerged lands may cross this threshold during the next 100 years under the RCP 8.5 scenario.

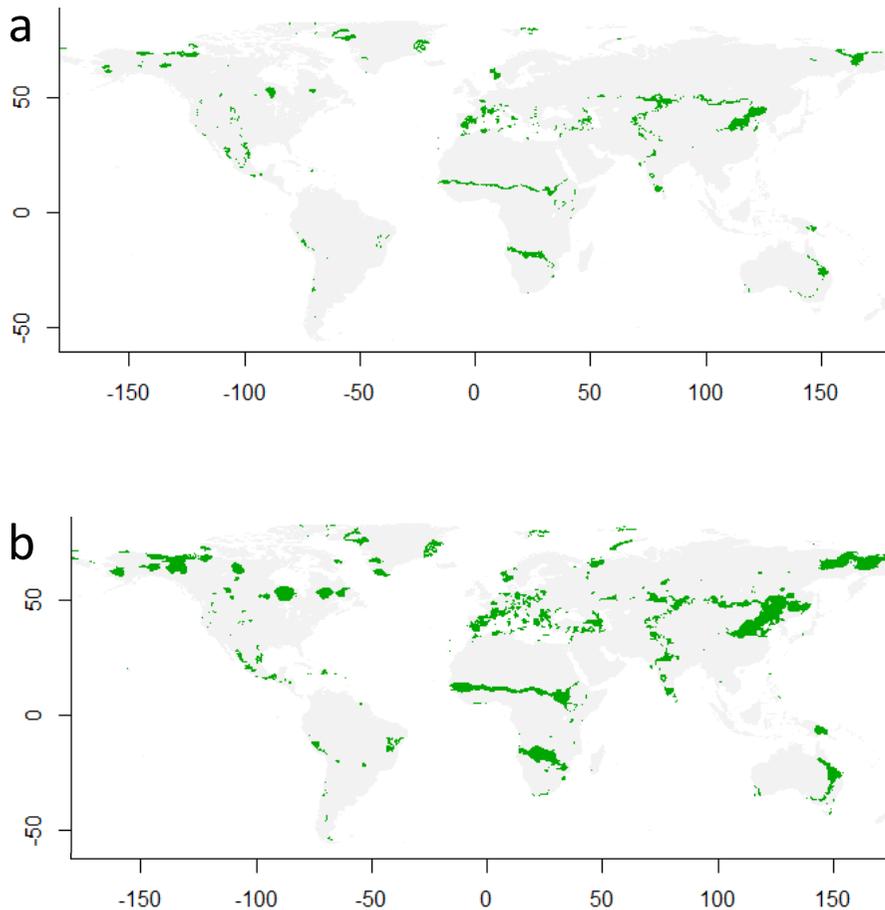


Figure 8.3. Forecasting threshold surpassing in the next 100 years.

The green areas represent zones where the aridity increments surpassed the aridity threshold found in this thesis (~ 0.7) in 2100 according to RCP 4.5 (a, assuming saturation of CO_2 increases) and RCP 8.5 (b, assuming exponential increase of CO_2) scenarios (Solomon 2007). Maps of aridity increases taken from Huang *et al.* (2015) were used to estimate aridity increases between 2012 and 2100 in both scenarios.

Zones identified include subtropical regions of Africa and South America, an important percentage of Australia and Asia, the northern parts of North America and several portions of southern Europe (Figure 8.3). Predictions of current climatic models (following RCP 4.5 and 8.5 for contrasting scenarios of increasing CO_2 concentration) also allowed us to track the possible dynamical behaviour of

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this process, which will not transform lands once and for all, but allow some years in which the threshold would be passed on and off (Figure 8.4). This is important as ecosystems may recover easier from critical transitions if the duration of the press that originated it is short (Ratajczak et al. 2017). This information can be used by land managers and policy makers to establish monitoring and mitigation actions, as our findings support the idea that abrupt and non-reversible changes in ecosystem structure and functioning may occur when the aridity threshold of 0.7 is crossed.

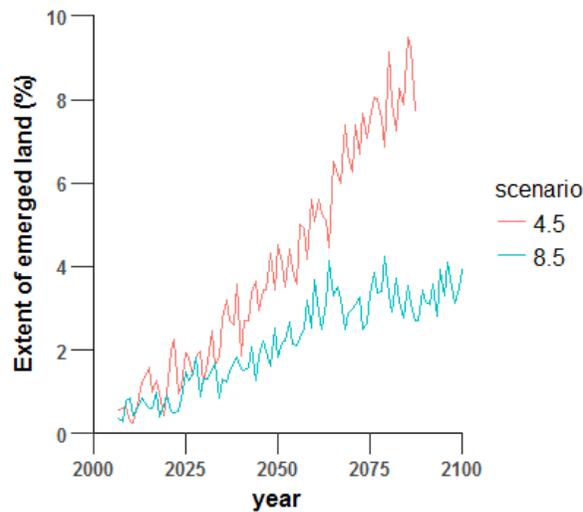


Figure 8.4. Extent of emerged lands affected by threshold surpassing in the next century.

Temporal changes of the extent of areas (in percentage respect to the total emerged lands) that will surpass an aridity threshold of 0.7 according to the IPCC RCP 4.5 and RCP 8.5 scenarios. Aridity estimates were obtained from Huang *et al.* (2015).

It is important to note that the aridity threshold identified here is based on a space-by-time substitution, and derive from using only a single (although global) dataset. As different regions might show a tight dependence on their species pool, independent regional gradients of aridity confirming the results of this thesis may help on strengthen the consistency of the patterns showed here, and also might enlighten whether other factors might affect aridity thresholds. Also, dynamical approaches (i.e., studies using temporal scales) should confirm the findings presented, as ecological responses obtained across spatial and temporal gradients

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may differ (Blois et al. 2013). In this regard, climate change might exert retarded effects on community structure (e.g., the vegetation that is already settled in communities might survive the new conditions imposed, Forti *et al.* 2006) even if it is unable to produce new seedlings (Castro et al. 2004, 2005, Lloret et al. 2012) or vegetation might even completely acclimate to these new conditions (Bradford et al. 2008, Somero 2010). Both are processes that are often disregarded in approaches such as ours, and that importantly affect the decisions that should be taken by land managers and policy makers. Also, using the space by time substitution approach, in this thesis I hypothesized that the introduction of specialists in new ecosystems may change the dynamics of the ecosystem and might be associated to drastic declines on ecosystem functioning. However, the introduction of new species specialized to arid sites in a community in which they were not there previously might create plant-plant interactions whose output is disregarded in a space by time substitution approach such as ours.

Future studies should also investigate the exact mechanisms involved in the threshold found in this thesis in order increase our understanding on how to promote actions to fight against it. For instance, if the main force operating abrupt changes in community structure, spatial pattern and functionality is plant-plant interactions, the introduction of species able to promote soil and microclimatic amelioration in arid conditions might attenuate patch destruction, increase functional diversity, and thus prevent ecosystem to loss functionality. There are already many studies devoted to use facilitation as a restoration tool (Maestre et al. 2001, Castro et al. 2002, Padilla and Pugnaire 2006, Byers et al. 2006, Pueyo et al. 2009), and this thesis stresses the fact that performing nurse-beneficiary studies for restoration and managing at both sides of threshold might be highly relevant to experimentally test the patterns found here (waning of facilitation effects on plant spatial patterns and the assembly of most species in the pool with aridity levels < 0.7, as they become specialized to aridity).

Finally, most of the communities analysed in this thesis are “natural” or “seminal” ecosystems. It is likely that grazing, fire or agriculture, would affect the threshold or feedback on its consequences, for instance by accelerating soil loss and avoiding specialists to colonize communities of the future, thus leading to desertified ecosystems. So, interactions of the aridity threshold identified here with other forms of land degradation, should be explored by further studies. In this

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regard, this thesis provides new hypotheses that should be considered. For instance, one of our hypothesis is that aridity levels higher than 0.7 affect the dynamics of ecosystems transforming equilibrium systems in non-equilibrium systems. In non-equilibrium ecosystems, the match between biomass production and grazers survival is of paramount importance (i.e., low rainfall years will result in low productivity that necessarily imply less survival of grazers, Ellis & Swift 1988). Thus, non-equilibrium rangelands need to be carefully managed to avoid the collapse of the ecosystem in years with low rainfall (Vetter 2005).

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Conclusiones



Conclusiones

Conclusiones

1. Existen dos tipos de patrones espaciales en los ecosistemas de zonas áridas. El primer tipo de distribución de manchas de vegetación se ajusta a una ley potencial (“power law”), y se caracteriza por la presencia de manchas grandes generadas por las interacciones planta-planta. El otro tipo de distribución de manchas se ajusta mejor a una distribución log-normal y se caracteriza por la ausencia de manchas grandes y su morfología depende principalmente de los tamaños de las especies que habitan en el ecosistema.
2. Encontramos dos tipos de ecosistemas entre los muestreados: los que tienen altos valores de funcionalidad, asociados a procesos que se relacionan con todos los nutrientes del suelo estudiados, y los que tienen bajos valores de funcionalidad, donde ésta se ve claramente restringida por la abundancia de elementos de origen biótico (carbono y nitrógeno). Estos tipos funcionales se relevan el uno al otro a lo largo de un gradiente de aridez y, notablemente, coocurren en niveles de aridez en torno a 0.7 (calculados como 1- índice de aridez sensu Middleton & Thomas, 1992), sugiriendo la existencia de estados alternativos estables en los ecosistemas de las zonas áridas.
3. Aunque la cobertura de plantas perennes es el mejor predictor de la multifuncionalidad, los dos tipos de patrones espaciales descubiertos son los únicos capaces de identificar el tipo funcional del ecosistema. Se encontró una asociación clara entre distribuciones de manchas de vegetación caracterizadas por leyes potenciales y alta multifuncionalidad, y entre distribuciones caracterizadas por una ecuación tipo lognormal y baja multifuncionalidad.
4. La importancia de la facilitación en el ensamblaje de las comunidades de zonas áridas decrece a lo largo de gradientes de aridez hasta niveles de aridez de 0.7. A estos niveles la importancia de la competencia entre especies toma el relevo como agente ensamblador de la comunidad. Este umbral coincide con la desaparición del efecto de las interacciones planta-planta en los patrones espaciales de la vegetación.
5. Los cambios en la importancia de la facilitación/competencia sobre el ensamblaje de las comunidades están asociados a modificaciones en el grado de especialización de las especies frente a la aridez. La mayoría de

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especies se hayan fuertemente especializadas a condiciones de extrema aridez a partir de un nivel de aridez = 0.7.

6. Aunque la importancia de la facilitación en el ensamblaje de comunidades colapsa a niveles de aridez muy elevados, ésta interactúa fuertemente con el grado de adaptación de las especies consideradas. Por tanto, la facilitación aún es importante para aquellas pocas especies mal adaptadas a las condiciones de aridez locales, particularmente para niveles de aridez superiores a 0.7.
7. La especialización de las comunidades se explica por un cambio en los rasgos funcionales de las especies, y esta relación interactúa fuertemente con la aridez. En niveles de aridez por debajo de 0.7 la especialización de las comunidades se halla asociada a rasgos típicos de especies tolerantes al estrés (baja altura y hojas coriáceas y pequeñas), mientras que a partir de niveles de aridez de 0.7 las comunidades están dominadas por arbustos más altos y con mayor superficie específica de la hoja (probablemente evitadoras de estrés).
8. Existe una relación significativa entre la especialización de las comunidades y la multifuncionalidad del ecosistema que interactúa con la aridez, siendo máxima para niveles de aridez superiores a 0.7.
9. El grado de especialización de la comunidad está fuertemente asociado con los estados estables de multifuncionalidad encontrados en las zonas áridas a escala global, siendo esta asociación incluso mayor que la existente entre los tipos de patrón espacial descritos previamente.



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