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SPECIAL FEATURE – EDITORIAL
GRASS–WOODLAND TRANSITIONS

Grass–woodland transitions: determinants and consequences for ecosystem functioning and provisioning of services

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Summary

1. A large fraction of grasslands world-wide is undergoing a rapid shift from herbaceous to woody-plant dominance, while in other parts of the world, the opposite transition from woodland to grassland is the dominant phenomenon. These shifts have received increasing attention in the ecological literature during the last two decades due to their global extent and their impacts on ecosystem functioning.
2. This Special Feature includes a series of contributions on key topics within the study of grass–woodland transitions, including three articles addressing the drivers of these vegetation shifts and another three evaluating their ecological consequences. These articles, which include reviews, modelling and empirical studies, highlight the multiplicity of approaches and spatial scales being currently used when studying grass–woodland transitions.
3. The first articles focus on the role of fire in driving the dynamics of mesic grasslands in the USA, on the effects of climate change on the transition zones between treeless vegetation, savanna and forest in tropical and subtropical Americas and on the role of the internal structure of vegetation as a determinant of grassland–woodland transitions. The articles devoted to exploring the consequences include a modelling study on the ecohydrological consequences of shrub removal in western North America and an empirical study aiming at understanding how abiotic and biotic attributes influence above-ground net productivity across Patagonian grasslands and shrublands, as well as a review of the consequences of brush management on the provision of ecosystem services.
4. *Synthesis*. Identifying the best actions to avoid or take advantage of grass–woodland transitions requires a mechanistic understanding of both the drivers of these shifts and their ecological consequences. The collection of reviews, empirical and modelling studies included in this Special Feature contributes to forecasting how ongoing global change will affect grass–woodland transitions and their consequences for the provisioning of ecosystem services from drylands, which account for a large fraction of Earth's surface.

Key-words: climate change, ecosystem services, ecosystem–water dynamics, fire, grasslands, invasion ecology, primary production, shrublands, vegetation shifts, woody-plant encroachment

Introduction

Grasslands, woodlands and savannas occupy large portions of the Earth's surface and are particularly prevalent in dry, temperate and tropical/subtropical regions (Loveland *et al.* 2000). These vegetation types play a key role in the functioning of the biosphere and in supporting the needs of the human population through the provision of multiple ecosystem services (Sala & Paruelo 1997; Havstad *et al.* 2007). An important part of the world's grasslands and savannas is undergoing a rapid shift from herbaceous to woody-plant dominance (Archer 2010). Just in North America, woody-cover increase ranges from 0.5% to 2% per year (Barger *et al.* 2011), and

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this fundamental alteration of habitat is among the major land-cover changes that have occurred over the past 150 years (Van Auken 2000). Managers have responded to this striking land-cover change with extensive brush control programmes such as Restore New Mexico in the USA (http://www.blm.gov/nm/st/en/prog/restore_new_mexico.html), which is a programme led by the US Bureau of Land Management that has treated 1.8 million acres with herbicides since 2005. The involuntary transformation of grasslands into woodlands described above contrasts against the purposeful transition in other parts of the world where land managers convert natural grasslands to plantations driven by market incentives such as wood production or carbon sequestration (Cubbage *et al.* 2007). Another human-driven transition is represented by the logging of woodlands that are converted into grasslands (Conant, Paustian & Elliott 2001).

The extent and ecological implications of the transitions among grasslands, woodlands and savannas have inspired interest in understanding the consequences of these changes for the functioning of the ecosystems (Van Auken 2000; Conant, Paustian & Elliott 2001; Barger *et al.* 2011; Eldridge *et al.* 2011; Ratajczak, Nippert & Collins 2012). For example, a recent meta-analysis of 244 case studies reported 10 significant structural and functional changes after woody encroachment of former grasslands in drylands, ranging from plant and animal diversity to primary production, total carbon, soil nitrogen and hydraulic conductivity (Eldridge *et al.* 2011). A recent study conducted in more than 200 drylands world-wide showed a unimodal effect of woody cover on plant species richness and ecosystem multifunctionality (Soliveres *et al.* 2014).

This Special Feature includes a series of reviews, modelling and empirical studies on key topics within the study of grass–woodland transitions, including three articles addressing the drivers of these vegetation shifts and another three evaluating their ecological consequences (Fig. 1). Below, we briefly discuss causes and consequences of grass–woodland transitions, highlighting how the different articles selected for this Special Feature contribute to filling in current gaps in our understanding.

Drivers of grass–woodland transitions

Climate is a key driver of the distribution of vegetation including, grasslands and woodlands (Bailey 2014). Along a gradient of precipitation, while maintaining temperature constant, the proportion of trees increases from grasslands, which have no trees, to savannas, which have a mixture of trees and grasses, to a closed-canopy forest (Bailey 2014). However, the effect of precipitation on the distribution of forest, savannas and treeless is not always linear. Studies of continental patterns have shown discontinuities in the distribution of woody-plant abundance with precipitation (Hirota *et al.* 2011). Grasslands show no tree cover, savannas 20% and closed-canopy forests 80% tree cover. However, the frequency of intermediate states is remarkably very small, highlighting the occurrence of precipitation-tipping points where ecosystem can easily shift from one physiognomic state to the other.

The ecological mechanisms behind the dominance of grasses or woody species are associated with the interactions between precipitation amount, seasonality and soil texture (Sala, Lauenroth & Golluscio 1997). Grass species tend to have shallower roots than shrubs (Jackson *et al.* 1996) and therefore have a competitive advantage in locations with a shallow distribution of soil water (Casper & Jackson 1997). In turn, distribution of soil water in the profile depends on precipitation amount, seasonality and texture. The same amount of precipitation penetrates deeper into a coarse-textured than in a fine-textured soil (Saxton & Rawls 2006). The seasonality of precipitation affects distribution of water in the soil profile, with ecosystems where precipitation occurs during the warm season having shallower water profiles than those where precipitation occurs during the winter. For example, North American Shortgrass Steppe and Patagonian Steppe represent two examples of semi-arid ecosystems with contrasting precipitation seasonality. The former has a water profile skewed towards the upper layers (Sala, Lauenroth & Parton 1992) with the 4–15 cm layer having the highest probability of being wet, whereas the latter, where 70% of the precipitation occurs during the cold months, the highest probability of being wet occurs in the deepest layers (Paruelo & Sala 1995). Thus, seasonality and texture largely determine a two-dimensional space, where woody vegetation dominates in the extreme of coarse texture and winter precipitation and grasses in the other extreme (Sala, Lauenroth & Golluscio 1997). In between these two extremes, there are areas that have low resilience, and ecosystems are vulnerable to shifts from grassland to woodland or vice versa.

Multiple studies have attempted to forecast how climate change will affect grassland and woodland distributions (Hutyra *et al.* 2005; Salazar, Nobre & Oyama 2007). While this body of evidence indicates that climate change will certainly affect the equilibrium between grass and woody vegetation, no study so far has explicitly evaluated how climate change will affect the transitions between forests, savannas and treeless areas at regional to continental scales. This was done by Anadón, Sala & Maestre (2014) in this Special Feature, who used models of current distribution of treeless vegetation, savanna and forest coupled with an ensemble of global circulation models, to forecast how climate change will affect the distribution of these vegetation types, and of the transition zones among them, in tropical and subtropical Americas. Their results indicate that climate change will promote a savannization of this region, with significant reduction in the area covered by forest and an expansion of the savanna vegetation type. In addition, there will be an expansion of transition zones, which will be vulnerable to land-use change. These transition zones will increase in size and will shift in location, up to 1000 km northwards.

The second article of the Special Feature (Ratajczak *et al.* 2014) presents a synthesis of a wealth of studies assessing the effect of fire intensity and frequency on grass–woodland dynamics in North American Tallgrass Prairie. Transition from grassland to shrubland is triggered by fire-free intervals, which facilitate recruitment of new individuals and new

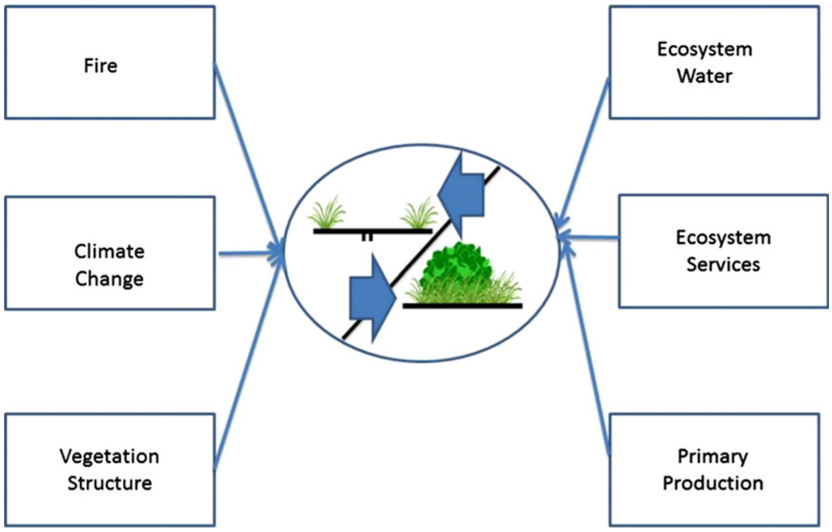

Fig. 1. Diagram of the Special Feature showing in the centre the dynamic relationship between grasslands and woodlands highlighting the bidirectionality of the phenomenon. The three boxes on the left show the articles depicting major drivers of the grass–woodland transition and the boxes on the right show the articles assessing the consequences of those transitions.

species of woody plants. Once established, subsequent periodic fires promote rapid expansion of clonal shrub species as a result of enhanced post-fire recruitment. Nonlinear transition and hysteresis occur because grasses, under high fire frequency, generate conditions that prevent establishment of woody plants. When the fire frequency is reduced, shrubs and trees become established. When woody plants get established, increased fire frequency does not reverse the process but further increases the dominance of woody plants.

Grass–woodland transitions constitute a particular example of abrupt changes in the distribution of vegetation across spatial gradients, which are ubiquitous in nature (Sasaki *et al.* 2008; Scheffer *et al.* 2012). Interestingly, patches of both woodlands and grasslands also show internal structure, such as banded patterns and the formation of clumps of different sizes that follow a power law distribution (Kefi *et al.* 2007; Deblauwe *et al.* 2008). These vegetation patterns have been extensively studied in dryland ecosystems from local to regional scales (Tongway & Ludwig 1990), albeit their role as a potential determinant of grass–woodland transitions has been poorly understood until now. In this Special Feature, Abades, Gaxiola & Marquet (2014) showed that the proportion of 40% tree cover and 60% grass cover, which is characteristic of savannas, results from a critical threshold associated with fire spread. Below 40% grass cover, fire does not spread and the system tips into a closed-canopy forest. And, above 40% grass cover, the system burns frequently and stays in the grassland domain. This novel modelling approach based on first principles nicely predicted fire-driven transitions between grasslands and woodlands.

Ecological consequences of grass–woodland transitions

Grasslands and woodlands produce a range of ecosystem services, which include food and fibre production, carbon sequestration, maintenance of the genetic library (conservation) and recreation (Sala & Paruelo 1997; Havstad *et al.* 2007). As vegetation shifts from grassland to woodland, the ecosystem services that they provide are also expected to change. Arid and semi-arid ecosystems were once used primarily for animal husbandry; wool and meat production were recognized as the most important ecosystem service provided by these regions (Yahdjian, Sala & Havstad 2014). A recent study based on census data and remote sensing imagery from North and South America showed that a 1% increase in woody-plant cover results in a 2.5% decrease in mean livestock production (Anadón *et al.* 2014). This result, coupled with the estimate of an increase in woody-plant cover in North America ranging between 0.5% and 2% per year (Barger *et al.* 2011), puts in perspective the huge importance of the phenomenon of woody-plant encroachment on the provisioning of ecosystem services.

As the supply of ecosystem services in rangelands has changed due to woody-plant encroachment, so has the demand for services (Yahdjian, Sala & Havstad 2014). For example in the USA, the demand for livestock forage in drylands has decreased by 14% from between 1979 and 2009. In land managed by the Bureau of Land Management areas, which administers a large fraction of drylands in the USA, the demand for forage since 1947 has decreased by 48% (Yahdjian, Sala & Havstad 2014). This change in demand varies among regions, while demand in the USA for livestock forage has been decreasing, globally, the number of cattle, sheep and goats increased by 600 million in the last 30 years (Estell *et al.* 2012). The decline in the demand of one type of ecosystem service is offset by increases in others. For example in the USA, demands for tourism and recreation in drylands increased, as assessed by the number of visitors, hunters and wildlife-watchers in arid public lands and National Parks (Cordell 2012). In synthesis, woody-plant encroachment affects the provisioning of ecosystem services, but its impact on humans depends also on the demand of ecosystem services, which varies among stakeholders, and changes through time and among regions. Therefore, it is easier to assess the impact of woody-plant encroachment on ecosystem processes and services than on well-being, which is determined by the balance of supply and demand of ecosystem services (Yahdjian, Sala & Havstad 2014).

Woody-plant encroachment represents a major challenge to the management of grassland and savanna ecosystems (du Toit, Walker & Campbell 2004). In drylands undergoing grass–woodland transitions, management actions aiming at improving the provisioning of services such as forage production and ground water recharge have focused on reducing the abundance of encroaching woody vegetation. In this Special Feature, Archer & Predick (2014) evaluated the consequences of brush management on a wide range of ecosystem services, ranging from forage production to biodiversity and habitat conservation. In addition, they assessed the scientific challenges to quantifying these services and their trade-offs. Despite considerable investments accompanying the application of brush management practices, the recovery of key ecosystem services such as forage production may be short-lived or absent. Predictions of ecosystem responses to brush management are limited for many attributes (e.g. primary production, land surface–atmosphere interactions, biodiversity conservation) and inconsistent for others (e.g. forage production, herbaceous diversity, water quality/quantity, soil erosion, carbon sequestration). Addressing the challenges posed by woody-plant encroachment requires a thorough understanding of the ecological mechanisms behind the phenomenon and of the cultural traditions, preferences and socio-economic constraints that may lead to competing land-use objectives. While this is certainly a challenging task, Archer & Predick (2014) provided a roadmap of priority areas for research that can reduce uncertainty and improve predictions of the outcomes of brush management activities.

Bio-physical theory of plant–soil–water dynamics suggests that grass–woodland transitions should result in important ecohydrological changes, such as alterations in soil–water availability, evaporation, transpiration and water yield (Sala, Lauenroth & Golluscio 1997; Huxman *et al.* 2005; Wilcox *et al.* 2012). Using an extensive data base with over 900 study sites coupled to an ecosystem–water balance model, Bradford *et al.* (2014) evaluated in this Special Feature the hydrological impacts of the removal of big sagebrush (*Artemisia tridentata*) in shrub-steppe ecosystems across western North America. These ecosystems provide habitat for many wildlife species, several of which are threatened or endangered, including sage grouse (*Centrocercus urophasianus*) and pygmy rabbits (*Brachylagus idahoensis*) and are used for livestock grazing. Sagebrush ecosystems over the past half a century have been subject to a range of shrub removal treatments to enhance wildlife habitat (Beck, Connelly & Wambolt 2012). Bradford *et al.* (2014) found that transitions from shrub to grass dominance decreased precipitation interception and transpiration, and increased soil evaporation and deep drainage. Relative to intact sagebrush vegetation, simulated soils in the herbaceous vegetation phase typically had drier surface layers and wetter deep layers. These findings provide important insights into the ecohydrological consequences of range management in a large region of North America.

Above-ground net primary productivity of natural vegetation (ANPP) is a critical ecosystem process that determines the provision of multiple ecosystem services, including livestock production, carbon sequestration, forage production and the maintenance of soil fertility (Oesterheld, Sala & McNaughton 1992; Sala & Paruelo 1997). While there is a good understanding of how climate controls ANPP of drylands at the regional to global scales (Sala *et al.* 1988, 2012), little is known about how vegetation attributes, in our case woody-plant cover, influence ANPP over large geographical areas. In this Special Feature, Gaitán *et al.* (2014) used 311 sites located across a broad natural gradient in Patagonian rangelands and structural equation modelling to evaluate the relative importance of climate (temperature and precipitation) and vegetation structure (grass/shrub cover and species richness) as drivers of ANPP. They found that climate and vegetation structure (grass/woody cover) explained over 70% of the variation found in ANPP.

Concluding remarks

This Special Feature stressed the complexity of grass–woodlands transitions resulting from multiple phenomena occurring at a broad range of scales. These transitions are driven by deliberate human actions, natural phenomena and the unintended consequences of management practices. This Special Feature did not attempt to cover the entire complexity of drivers and consequences of grass–woodland transitions. For example, studies of social and economic drivers of the grass–woodland transitions are not represented here. Instead of thoroughness, the Special Feature offers highlights of important studies of grass–woodland transitions using a variety of approaches from synthesis and field experiments to simulation modelling and remote sensing.

The challenge for the next generation of studies of grass–woodland transitions is the integration of different approaches, disciplines, methods, conceptual frameworks and scales. All approaches and scales need to be taken into consideration to fully understand the phenomenon and contribute to the design of optimal management strategies. However, these disparate approaches need to be integrated under a common conceptual framework. Challenges of interdisciplinary research are not unique to the issue grass–woodland transitions and result from the difficulties of overcoming different conceptual backgrounds as well as institutional barriers. Progress towards integration sometimes results from interdisciplinary meetings where people with disparate backgrounds who are working on a common subject get together. This Special Feature emerged from a workshop at the South American Resilience and Sustainability Science (SARAS) in Maldonado, Uruguay, and the support of multiple institutions from Uruguay, the USA and Europe. The difficulties of integration increase with the dissimilarity of disciplines; it is easier to integrate different disciplines within the physical sciences than to integrate social and natural sciences. This Special Feature unites elements of soil physics and biology focusing on management and ecosystem services, which are areas of knowledge, rooted in the humanities and social sciences. Institutions from journals to funding agencies in some cases have been hesitant to embark on interdisciplinary projects. We hope that the workshop and this Special Feature will motivate further interdisciplinary studies and a new kind of research on grass–woodland transitions that will yield novel understanding and management approaches to meet the increasing and contrasting demands on arid and semi-arid ecosystems.

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References

Abades, S., Gaxiola, A. & Marquet, P. (2014) Fire, percolation thresholds and the savanna forest transition: a neutral model approach. *Journal of Ecology*, **102**, 1386–1393.

Anadón, J.D., Sala, O.E. & Maestre, F.T. (2014) Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *Journal of Ecology*, **102**, 1363–1373.

Anadón, J.D., Sala, O.E., Turner, B.L. & Bennett, E.M. (2014) Effect of woody plant encroachment on livestock production: a comparison of North and South America. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 12948–12953.

Archer, S. (2010) Rangeland conservation and shrub encroachment: new perspectives on an old problem. *Wild Rangelands: Conserving Wildlife while Maintaining Livestock in Semi_arid Ecosystems* (eds J. du Toit, R. Kock & J. Deutsch), pp. 53–97. Wiley-Blackwell, Oxford.

Archer, S. & Predick, K. (2014) An ecosystem service perspective on brush management: research priorities for competing land-use objectives. *Journal of Ecology*, **102**, 1394–1407.

Bailey, R.G. (2014) *Ecoregions: The Ecosystem Geography of the Oceans and Continents*. Springer, New York, NY.

Barger, N.N., Archer, S.R., Campbell, J.L., Huang, C.Y., Morton, J.A. & Knapp, A.K. (2011) Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research*, **116**, G00K07.

Beck, J.L., Connelly, J.W. & Wambolt, C.L. (2012) Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. *Rangeland Ecology and Management*, **65**, 444–455.

Bradford, J.B., Schlaepfer, D., Lauenroth, W.K. & Burke, I.C. (2014) Ecohydrological consequences of plant functional type transitions in North American sagebrush ecosystems. *Journal of Ecology*, **102**, 1408–1418.

Casper, B.B. & Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, **28**, 545–570.

Conant, R.T., Paustian, K. & Elliott, E.T. (2001) Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications*, **11**, 343–355.

Cordell, H. (2012) *Outdoor Recreation Trends and Futures: A Technical Document Supporting the Forest Service* (ed. R. A. G. T. R. SRS-150), pp. 167. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC.

Cubbage, F., Mac Donagh, P., Sawinski Junior, J., Rubilar, R., Donoso, P., Ferreira, A., Hoeflich, V., Olmos, V.M., Ferreira, G. & Balmelli, G. (2007) Timber investment returns for selected plantations and native forests in South America and the Southern United States. *New Forests*, **33**, 237–255.

Deblauwe, V., Barbier, N., Couteron, P., Lejeune, O. & Bogaert, J. (2008) The global biogeography of semi-arid periodic vegetation patterns. *Global Ecology and Biogeography*, **17**, 715–723.

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

Estell, R., Havstad, K.M., Cibils, A., Anderson, D., Schrader, T. & James, K. (2012) Increasing shrub use by livestock in a world with less grass. *Rangeland Ecology and Management*, **65**, 553–562.

Gaitán, J., Oliva, G., Bran, D., Maestre, F.T., Aguiar, M.R., Jobbágy, E., Buono, G., Ferrante, D., Nakamatsu, V., Ciari, G., Salomone, J. & Massara, V. (2014) Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. *Journal of Ecology*, **102**, 1419–1428.

Havstad, K.M., Peters, D.P.C., Skaggs, R., Brown, J., Bestelmeyer, B.T., Fedrickson, E., Herrick, J.E. & Wright, J. (2007) Ecological services to and from rangelands of the United States. *Ecological Economics*, **64**, 261–268.

Hirota, M., Holmgren, M., Van Nes, E.H. & Scheffer, M. (2011) Global resilience of tropical forest and Savanna to critical transitions. *Science*, **334**, 232–235.

Hutyra, L.R., Munger, J.W., Nobre, C.A., Saleska, S.R., Vieira, S.A. & Wofsy, S.C. (2005) Climatic variability and vegetation vulnerability in Amazonia. *Geophysical Research Letters*, **32**, L24712.

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T. & Jackson, R.B. (2005) Ecohydrological implications of woody plant encroachment. *Ecology*, **86**, 308–319.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.

Kefi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A. & de Ruiter, P.C. (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, **449**, 213-U5.

Loveland, T.R., Reed, B.C., Brown, J.F., Ohlen, D.O., Zhu, Z., Yang, L. & Merchant, J.W. (2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. *International Journal of Remote Sensing*, **21**, 1303–1330.

Oesterheld, M., Sala, O.E. & McNaughton, S.J. (1992) Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, **356**, 234–236.

Paruelo, J.M. & Sala, O.E. (1995) Water losses in the Patagonian steppe: a modelling approach. *Ecology*, **76**, 510–520.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, **93**, 697–703.

Ratajczak, Z., Nippert, J.B., Briggs, J.M. & Blair, J.M. (2014) Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *Journal of Ecology*, **102**, 1374–1385.

Sala, O.E., Lauenroth, W.K. & Golluscio, R.A. (1997) Plant functional types in temperate semi-arid regions. *Plant Functional Types* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 217–233. Cambridge University Press, Cambridge.

Sala, O.E., Lauenroth, W.K. & Parton, W.J. (1992) Long term soil water dynamics in the shortgrass steppe. *Ecology*, **73**, 1175–1181.

Sala, O.E. & Paruelo, J.M. (1997) Ecosystem services in grasslands. *Nature's Services: Societal Dependence on Natural Ecosystems* (ed. G.C. Daily), pp. 237–252. Island Press, Washington, DC.

Sala, O.E., Parton, W.J., Lauenroth, W.K. & Joyce, L.A. (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.

Sala, O.E., Gherardi, L., Reichmann, L., Jobbágy, E. & Peters, D. (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **367**, 3135–3144.

Salazar, L.F., Nobre, C.A. & Oyama, M.D. (2007) Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, **34**, L09708.

Sasaki, T., Okayasu, T., Jamsran, U. & Takeuchi, K. (2008) Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *Journal of Ecology*, **96**, 145–154.

Saxton, K.E. & Rawls, W.J. (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal*, **70**, 1569–1578.

Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H. & Chapin, F.S. (2012) Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 21384–21389.

Soliveres, S., Maestre, F.T., Eldridge, D.J., Delgado-Baquerizo, M., Quero, J.L., Bowker, M.A. & Gallardo, A. (2014) Plant diversity and ecosystem multifunctionality peak at intermediate levels of woody cover in global drylands. *Global Ecology and Biogeography*, doi:10.1111/geb.12215.

du Toit, J.T., Walker, B.H. & Campbell, B.M. (2004) Conserving tropical nature: current challenges for ecologists. *Trends in Ecology & Evolution*, **19**, 12–17.

Tongway, D.J. & Ludwig, J.A. (1990) Vegetation and soil patterning in semi-arid mulga lands of Eastern Australia. *Australian Journal of Ecology*, **15**, 23–34.

Van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.

Wilcox, B.P., Turnbull, L., Young, M.H., Williams, C.J., Ravi, S., Seyfried, M.S., Bowling, D.R., Scott, R.L., Germino, M.J., Caldwell, T.G. & Wainwright, J. (2012) Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology*, **5**, 160–173.

Yahdjian, L., Sala, O.E. & Havstad, K.M. (2014) Ecosystem services in rangelands: paradigm shift from focus on supply to balancing demand with supply. *Frontiers in Ecology and the Environment*, In press.

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