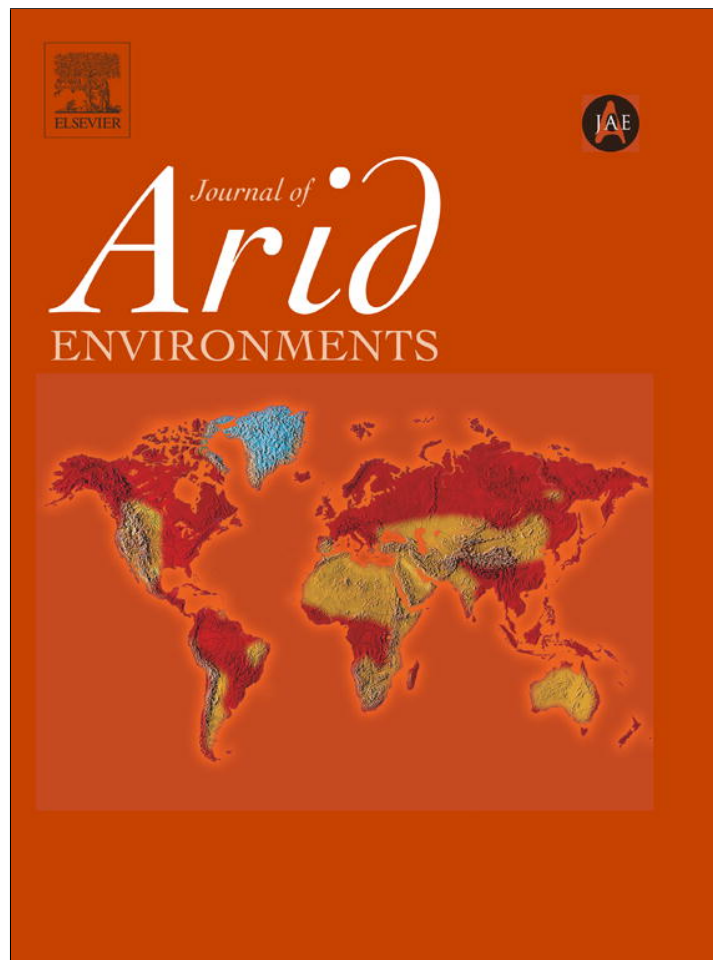


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

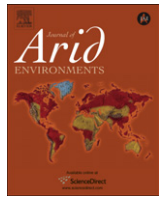
Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Review

Mammal functional diversity loss under human-induced disturbances in arid lands

V. Chillo*, R.A. Ojeda

Grupo de Investigaciones de la Biodiversidad (GiB), Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA) – CONICET, CCT-Mendoza, CC507, CP5500 Mendoza, Argentina

ARTICLE INFO

Article history:

Received 11 November 2011

Received in revised form

25 April 2012

Accepted 14 June 2012

Available online

Keywords:

Biodiversity measure

Ecosystem functioning

Effect traits

Land use change

Meta-analysis

ABSTRACT

Human activities are drastically changing the composition of mammal communities and increasing species local extinctions. Although it is well recognized that species influence the way in which ecosystems function through the diversity of resource use traits, little is known regarding the consequences of ecosystem functioning on changing biodiversity. We summarized studies that analyzed the effects of anthropogenic disturbances on mammal assemblages in arid and semi-arid lands of the world. We analyze for the first time changes in functional diversity values under a wide variety of disturbances using a meta-analysis.

General mean effect size was significantly negative and marginally heterogeneous. Grouping into ecosystems showed a varied response, mostly negative but not significant. When considering disturbance types as moderator factor, functional diversity responds in a negative way to all types, but the strongest effects were seen when we analyzed the mechanism by which disturbance affects ecosystem. 'Herbivory' effect was the least aggressive, and contrary, 'species change' strongly and negatively affected functional diversity. When disturbance generates changes in species and resources, and new state properties highly differ from the initial state property, the regime shift seen in vegetation has drastic consequences over mammal functional diversity. This loss of functional diversity may generate positive feedbacks that help to maintain degraded states of the ecosystem.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Human activities have, and continue to, change the environment at local and global scales. These activities are drastically leading to changes in the structure and composition of ecological communities and can cause biodiversity loss (Scheffer and Carpenter, 2003). Concern has arisen regarding the consequences that such biodiversity loss can have on the way ecosystem functions. After almost two decades of scientific research, it is accepted that changing biodiversity may affect ecosystem functions such as productivity and nutrient cycling (Cardinale et al., 2006; Loreau et al., 2002). Ultimately, these changes affect the goods and services that ecosystems provide to human well-being (Chapin et al., 2000; Millennium Ecosystem Assessment, 2005). Research trying to understand how changes in biodiversity affects ecosystem functioning has focused mainly on plant communities (Cardinale et al., 2006; Hooper et al., 2005; Tilman et al., 2002). Although

researchers are increasingly striving to integrate studies of biodiversity and ecosystem functioning with trophic structure in order to achieve a better understanding of energy flow and nutrient cycling in the ecosystem, there is little information regarding the relationship between animal diversity and ecosystem functioning (Duffy, 2003). Recent investigations including trophic levels and interactions between levels show that the identity of the species and the strength of interactions seem to be more important in maintaining ecosystem function than diversity at higher trophic levels (Cardinale et al., 2006; Duffy et al., 2007). Moreover, disturbances can alter extinction order (i.e. species with large body tend to be more extinction-prone), and these non-random responses of communities to disturbances can have unexpectedly large functional consequences (Larsen et al., 2005; Petchey and Gaston, 2002). Nevertheless, this topic has been studied mainly through mathematical models and in highly productive habitats, being the role of diversity in dry lands one of the least understood processes among different terrestrial ecosystems (Shachak et al., 2005).

Deserts are stressful environments where annual water loss due to evapotranspiration exceeds that which is gained by precipitation (Whitford, 2002), but still manage to support a surprisingly diverse fauna adapted to these constraints

* Corresponding author. Tel.: +54 261 5244130.

E-mail address: vcillo@mendoza-conicet.gov.ar (V. Chillo).

(Mares, 1992; Whitford, 2002). It has been proposed that consumers in deserts play an important role as regulators of ecosystem processes, affecting energy flow and nutrient cycling through direct and indirect effects, interactions and feedbacks (Bertiller et al., 2009; Noy-Meir, 1979, 1974). For example, the digging activity of some mammals for food and/or nesting leads to an increase in enriched soils as they move large amounts of organic matter from above to below ground. Also, these tunnels may increase water infiltration and can function as litter and seed traps that create nutrient-rich spots and safe germination sites (Whitford, 2002). Herbivores may modify plant composition, growth forms and productivity, shift carbon allocation patterns, consume and disperse seeds, ultimately affecting primary productivity (Bardgett and Wardle, 2003). Also, desert fauna may regulate energy flow through complex trophic interactions as a product of dominant opportunistic and generalistic behavior of consumers, with many within and across trophic level interactions that change in space and time (Noy-Meir, 1974; Polis, 1991; Shachak et al., 2005; Whitford, 2002). These are key topics to keep in mind when analyzing how animal biodiversity affects the functioning of ecosystems (Duffy et al., 2007).

Desert organisms are constantly exposed to extreme and unpredictable environmental factors, thus sometimes occurring at the limits of their tolerance ranges (Walker et al., 1999). Human-induced disturbances are common, persistent and usually intense, and disturbances such as logging, fire, agriculture expansion and livestock grazing, which can result in habitat lost and fragmentation, are the most common production strategies in arid lands, with consequent biodiversity losses (Reynolds et al., 2007). Although the response of mammals to disturbance depends on the characteristics of the disturbance and the habitat requirements of each species, most studies in arid lands have identified a decrease in the abundance of species and sometimes even local extinctions (Tabeni and Ojeda, 2003). Also, the slow recovery mainly associated with low and unpredictable rainfall, makes deserts more vulnerable to further disturbances (Walker et al., 1999). Ultimately, the synergy of these factors triggers desertification, which is the loss of fertile soil, above-ground biomass and biodiversity due to the detriment of processes such as nutrient cycling (Reynolds et al., 2007).

Understanding the consequences of biodiversity loss requires that we incorporate a functional comprehension of the ecosystem (Chapin et al., 2000). Changes in richness, abundances and species composition due to disturbances may have large functional consequences, and when affecting fauna, such changes are likely to have cascading and long-term effects throughout the ecosystem (Larsen et al., 2005). Nevertheless, recent studies in dry lands have focused on the effect of disturbances on the structure of the ecosystem, concentrating mainly on population and community changes, without going deeper into the consequences of these changes on ecosystem functioning. As the intensification of human activities increases over arid and semi-arid lands, it is important to understand the relationship between biodiversity and ecosystem functioning in order to predict and prevent catastrophic shifts (Reynolds et al., 2007; Scheffer and Carpenter, 2003). To contribute to this need, we aim to review current knowledge of the consequences of disturbances on the diversity of mammals in arid and semiarid lands, and to analyze this information with a functional diversity approach. For this, our objectives were to 1) review studies that analyzed disturbance effect on mammal assemblages in arid and semiarid lands worldwide, and 2) assess species traits of resource capture and use and analyze changes in functional diversity under different land use intensities.

2. Material and methods

2.1. Database search

We conducted an extensive search of published literature and identified studies that analyzed changes in the abundance of two or more mammals under different human-induced disturbances in arid and semiarid lands of the world. Then, we identified each mammal's functional traits in order to quantify the value of functional diversity of the selected assemblages under different types of disturbance. Finally, we performed a meta-analysis in order to assess the mean effect of disturbance on mammal's functional diversity.

We searched for publications in electronic databases (Scielo, Scopus, Elsevier and Blackwell) using different combinations of the following keywords: 'mammal', 'desert', 'arid', 'disturbance', 'grazing', 'poaching', 'hunting', 'logging', 'fire', and 'desertification'. We also searched for thesis manuscripts in Universities and used information given by colleagues. Overall, we only considered studies that reported the abundances of two or more mammal species under different disturbance intensities.

2.2. Functional diversity and disturbance assessment

We considered a 'functional trait' to be a characteristic of the organism that can be relevant to its effect on ecosystem functioning or its response to environmental fluctuations (natural or human-induced) (Díaz and Cabido, 2001). We selected traits for which information was available for all the species included in the analysis, and focused on resource capture and use traits, which influence the fitness of a species and the way in which the species is involved in the process of matter and energy flow (Flynn et al., 2009). For example, feeding guild and body mass reflect the type and amount of resources that species consume and release. Characteristics referring to species behavior are also important, because traits as activity pattern reflect the temporal distribution of resource use; while habitat use and home range strongly influence the spatial distribution and extent of resources intake and release (Flynn et al., 2009). The range or categories of selected traits (Table 1) reflect the functional diversity of the community in relation to the process of matter and energy flow. The species \times traits matrix was based on published information about the natural history of species.

We calculated a functional diversity value for each study that reported changes in the abundance of two or more species under different disturbance intensities. The reported abundances (when absolute) were relativized within disturbance intensities at each study. Quantification of functional diversity was done using Rao quadratic entropy (FD_Q) (Botta-Dukát, 2005), because, contrary to other common measures of functional diversity (i.e. FD *census* Petchey and Gaston, 2006) it allowed us to consider species relative abundance. This is an important factor to be considered because under low and moderate levels of disturbance, many mammal

Table 1
Traits and categories used for functional diversity assessment.

Traits	Range or categories
Body mass	Continuous (gr.)
Feeding guild	Carnivore, Insectivore, Herbivore, Granivore, Omnivore
Activity	Diurnal, Nocturnal
Habitat use	Arboreal, Terrestrial, Ground-dwelling, Fossorial, Semi-fossorial
Home range	Small (<1000 m ²), Medium (1000–10,000 m ²), Large (>10,000 m ²)

species respond by changing their abundance, and community responses are characterized by changes in relative composition, not in richness (Tabeni and Ojeda, 2003). As FD_Q does not fully associate to the evenness components, rather to functional richness and divergence, it is useful for the analysis of assemblages that presents smaller number of species than number of traits (Mouchet et al., 2010).

We consider a disturbance as a relatively discrete event in time that disrupts ecosystem, community or population structure and changes resource availability or the physical environment (White and Pickett, 1985). But this broad definition does not specify the particularities of different ecosystem characteristics, the interaction of different disturbance types in time and space, the feedbacks that maintain ecosystem properties and the potential non-linearity of ecosystem dynamic. In order to achieve a better understanding of disturbance effects in complex systems, and being able to make a cross-ecosystem comparison it is necessary to standardize disturbance characteristics. Peters et al. (2011) proposed a disaggregated view of disturbance analysis, which considers three measurable components: environmental drivers, initial and changed system properties, and physical and biological mechanism of effect. In this review we focus on anthropogenic drivers of disturbance and characterize type, amount and duration when reported. Within these, we characterized the initial properties and the mechanism of effect in the ecosystem (i.e. vegetation structure and composition). Initial system properties interact with drivers and mechanisms to result in legacies of the event which determine future ecosystem state. Nevertheless, this information was not always available, thus we included in the standardization only when it was reported by the authors. For each situation (41) identified in each publication (24) we characterized the disturbance according to the standardization proposed by Peters et al. (2011): 'relatively discrete' events should be described based on duration of a driver, or time over which a mechanism operates; and 'ecosystem disruption' as an alteration of the system that removes or adds structural components through the effect of drivers and mechanisms interaction with initial system properties to result in an outcome different from the reference state.

To evaluate if there is an effect of disturbances on functional diversity, we calculated an individual effect size value for each study and a cumulative effect size for all studies, using the results of the quantification of functional diversity. For each study, we obtained a mean value and number of replicates reported of the different treatments (disturbance characterizations). We selected Hedges' d effect size metric, which is an estimate of the standardized mean difference between treatments and is not biased by small sample size (Hedges and Olkin, 1985). The individual effect size value ' d ' (its variance ' $\text{Var}(d)$ ') was calculated based on pairwise comparisons between treatments. Positive effect values imply higher functional diversity in disturbed sites than in control (not disturbed sites), while negative values imply a negative effect of disturbance on functional diversity. To assess the overall effect of disturbance on functional diversity, we performed a conventional meta-analysis using a random-effect model (Gurevitch and Hedges, 1999). For this, we first tested our data for normality with a normal quantile plot. Also, heterogeneity in the magnitude of effect sizes (observed variation vs. variation intra-study) was tested using the statistics ' Q ', which tests the null hypothesis that there is homogeneity in the effect size of the studies analyzed, using a Chi-squared distribution (Rosenberg et al., 2000). Finally, we calculated 95% confidence intervals (CI) around the effect size, and considered a significant overall grand mean effect size (d_{++}) if confidence intervals did not overlap with zero. These analyses were done using METAWIN 2.0 statistical program (Rosenberg et al., 2000).

3. Results

We found 25 studies that evaluated the effect of human-induced disturbances on the abundance of two or more mammals of arid and semiarid lands (Appendix S1). Although more studies were identified, we could not use them because they did not reported species abundance. Our final data set comprises 110 species and the compilation of 5 traits per species (Appendix S2), of studies that reported observational results in a research period of 27 years (1983–2012), and in deserts of North America, South America, Australia and Africa. From the 25 studies that reported changes in abundances as a response to human-induced disturbance, we were able to differentiate 41 situations based on different types of disturbance (Table 2). Most of the studies explicitly described the size/amount of disturbance, initial state (before the disturbance, or paired control treatments) and the new state properties of the ecosystem, but there were also others who did not report this information (Table 2). This lack of information limited the extent of a qualitative cross-ecosystem comparison of disturbances. Nevertheless, the available information allowed the characterization of disturbances and the identification of potential moderator factor for the meta-analysis.

When analyzing all the data set together, the overall grand mean effect size was negative and confidence intervals didn't overlap with zero ($d_{++} = -0.49$; 95% CI = -0.75 to -0.22) (Fig. 1). Also, results showed no deviation from linearity and the heterogeneity test was not significant ($Q_b = 40.75$; $p = 0.39$). But the lack of significance of this test does not always mean that the effect sizes are homogeneous. Heterogeneity could be masked by the low power of the test when there is a great variance intra-study, given by low number of replicates (independent samples) within each study. In order to explore if other factor(s) may underlay the observed variation in functional diversity response, we further performed the calculation of cumulative effect size by grouping the studies into three moderator variables: Ecosystem (Fig. 2a), Disturbance type (Fig. 2b) and Mechanism Effect (Fig. 2c). We could not use initial state and new state properties as moderator variables because of the lack of information in some studies (Table 2).

When grouping into ecosystems we found a variety of responses, most of them with a negative trend but with no significant effect (Fig. 2). Mojave (USA) and Central Monte Desert (Argentina) shows the higher number of studies, but in the first desert there is a mean negative and significant effect size of disturbance over mammals functional diversity ($d_+ = -0.72$; CI = -1.39 , -0.06); while no significance was found for the second arid land ($d_+ = -0.28$; CI = -0.78 , 0.31). There were marginal differences in the way mammal functional diversity responds to disturbance between different ecosystems (Q_b , Fig. 2a). When considering disturbance types as moderator factor, mammal functional diversity respond in a negative way to all types. Also, there was no heterogeneity detected in the response of mammal functional diversity to disturbance types (Q_b , Fig. 2b). Finally, mammal functional diversity differs more in the way it responds to the mechanism by which disturbance affects ecosystem more than in the response to other moderator factors, although it wasn't statistically significant (Q_b , Fig. 2c). Here again, all responses were negative, but the majority were significant (confidence intervals didn't overlap with zero value).

4. Discussion

Our results show that human-induced disturbances negatively affect functional diversity of mammals in arid and semiarid biomes worldwide. We analyzed a wide range of case-studies representing different arid regions and incorporated the intrinsic complexity of

Table 2
Detailed characterization of the 41 disturbance events driven by anthropogenic activities used for the analysis. References are presented in Appendix S1.

Reference	Ecosystem	Disturbance event	Amount/size	Duration/return interval	Mechanism by which disturbance effects ecosystem	Initial state properties	New state properties
Beever and Brussard 2000	Great Basin (USA)	Grazing	±4.8 feral horses/ha	Constant	Grass herbivory/ shrub defoliation	Low bare soil cover/high vegetation cover	↓ vegetation cover/ ↓ species richness
Blaum et al., 2007	Kalahari (S.Africa)	Shrub encroachment	4 livestock unit/100 ha	Constant	Grass herbivory/ shrub redistribution	4–9% shrub cover	10–18% shrub cover
Blaum et al., 2007	Kalahari (S.Africa)	Shrub encroachment	6 livestock unit/100 ha	Constant	Grass herbivory/ species change	4–9% shrub cover	19–26% shrub cover
Brooks, 1995	Mojave (USA)	Grazing	<i>nr</i>	Constant since ±1800 s	Grass herbivory/ shrub defoliation	12–199 kg/ha annual/29.3% shrub cover/107–193 kg/ha seeds	5–58 kg/ha annual/19.4% shrub cover/50–56 kg/ha of seeds
Donadio and Buskirk, 2005	Puna (Arg)	Poaching	<i>nr</i>	Constant	Species change/ resource change	<i>nr</i>	<i>nr</i>
Eccard et al., 2000	Semi-arid Karoo (S.Africa)	Grazing	<i>nr</i>	Constant	Grass herbivory/ shrub defoliation	53–66% vegetation cover/ 1–2 m height shrubs	24–41% vegetation cover/ ↓ shrub height
Gonnet, 1998	Central Monte (Arg)	Grazing	Intense	Constant	Grass herbivory/ shrub redistribution	>30% total grass/10% 50 cm height grass cover	↓ total grass/1% 50 cm height grass cover/↑ bare soil
Gonnet, 1998	Central Monte (Arg)	Logging	<i>nr</i>	<i>nr</i>	Species change/ resource change	<i>nr</i>	<i>nr</i>
Hoffmann and Zeller, 2005	Nama Karoo (Namibia)	Grazing	<i>nr</i>	Constant	Grass herbivory/ shrub defoliation	10% dominant grass cover/ 2.5% shrub cover	Marked ↓ grass cover/ 2.1% shrub cover
Horn et al., 2012	Mojave (USA)	Old fire (5 yr)	712–27,059 ha	<i>nr</i>	Species change/ resource change	<i>nr</i>	<i>nr</i>
Jones and Longland, 1999	Great Basin (USA)	Grazing	85–143 feces/km transect	Constant	Grass herbivory/ shrub defoliation	53–70% shrub/km ² / 66–72% cryptogamic crust	26–82% shrubs/km ² /↑ exotic annuals/↓ crypt. crust cover
Joseph et al., 2003	Chihuahua (USA)	Grazing	35 vs. 45% use of forage	Constant	Grass herbivory/ shrub defoliation	242 kg/ha of grass/4.5% shrub/0.6% forbs cover	208 kg/ha of grass/3.3% shrub/ 0.4% forbs cover
Joubert and Ryan, 1999	Succulent Karoo (S.Africa)	Grazing	<i>nr</i>	Constant- nomadic for 2000 years	Grass herbivory/ shrub defoliation	39.8–41.4% shrub cover/ 0.1–1.7% annual cover/ 21.4–37.8% of ≥15 cm high	17.6–32.4% shrub cover/0.9–4.9% annual cover/7–28.4% of ≥15 cm high
Killgore et al., 2009	Chihuahua (USA)	Recent fire	±20 ha	<i>nr</i>	Species change/ resource change	≥10% cover dominant grass/ sparse shrub cover	≥4% cover dominant grass/↓ shrub canopy
Killgore et al., 2009	Chihuahua (USA)	Old fire (1 yr.)	±20 ha	<i>nr</i>	Species change/ resource change	≥10% cover dominant grass/ sparse shrubs	Recover 10–100% shrub canopy
Kutt and Woinarski, 2007	Desert upland (Aus)	Grazing	4–8 ha/livestock unit	Constant	Grass herbivory/ shrub defoliation	25% bare soil/65.8% grass/ 2.8% forbs cover	40.6% bare soil/48% grass but ↑ unpalatable cover
Kutt and Woinarski, 2007	Desert upland (Aus)	Old fire (2 yr.)	<i>nr</i>	<i>nr</i>	Species change/ resource change	25% bare soil/65.8% grass/ 2.8% forbs cover	55.7% bare soil/36.3% grass/ 3% forbs cover
Kutt and Woinarski, 2007	Desert upland (Aus)	Old fire (2 yr.) + grazing	4–8 ha/livestock unit	<i>nr</i>	Species change/ resource change/ grass herbivory	25% bare soil/65.8% grass/ 2.8% forbs cover	70% bare soil/17.2% grass/ 8% forbs cover
Letnic and Koch, 2010	Strezelecki (Aus)	Top predator exclusion	<i>nr</i>	Constant	Species change/ resource changes	Spread trees, shrubs, perennial vegetation	<i>nr</i>
Letnic et al., 2005	Simpson (Aus)	Recent fire	Intense/>10,000 km ²	<i>nr</i>	Species change/ resource change	60% total plant/ ±40% spinifex/ ±5% shrub cover	10% total plant/±5% spinifex grassland cover
Letnic et al., 2005	Simpson (Aus)	Recent fire (4 months)	Intense/>10,000 km ²	<i>nr</i>	Species change/ resource change	60% total plant/ ±40% spinifex/ ±5% shrub cover	20% total plant/±10% spinifex grassland cover
Letnic et al., 2005	Simpson (Aus)	Old fire (>25 yr.)	Intense >10,000 km ²	<i>nr</i>	Species change/ resource change	60% total plant/± 40% spinifex/ ±5% shrub cover	60% total plant/±30% spinifex/± 10% shrub cover
Mathis et al., 2006	Chihuahua (USA)	Shrub removal	Intense	Constant	Species changes/ resource changes	>50% grass cover	<i>nr</i>

Mathis et al., 2006	Chihuahua (USA)	Shrub removal + Grazing	Intense + 50% use of forage	Seasonal grazing	Species changes/ resource changes/ grass herbivory	>50% grass cover	nr
Ojeda, 1989	Central Monte (Arg)	Recent fire	Border of 60 ha	Un-common	Species changes/ resource changes	Shrub dominated/ scattered trees	nr
Ojeda, 1989	Central Monte (Arg)	Recent fire	Inside of 60 ha	Un-common	Species changes/ resource changes	Shrub dominated/ scattered trees	nr
Ojeda, 1989	Central Monte (Arg)	Old fire (1 yr.)	Border of 60 ha	Un-common	Species changes/ resource changes	Shrub dominated/ scattered trees	nr
Ojeda, 1989	Central Monte (Arg)	Old fire (1 yr.)	Inside of 60 ha	Un-common	Species changes/ resource changes	Shrub dominated/scattered trees	nr
Osteja and Schupp, 2009	Great Basin (USA)	Exotic grass invasion	±40,000,000 ha	nr	Species changes/ resource changes	45% grass/15% forbs/ 40% shrub cover	<i>Bromus tectorus</i> comprises >90% of standing biomass
Pereira et al., 2011	South-central Monte (Arg)	Grazing	nr	Constant	Grass herbivory/ shrub redistribution	Low bare soil/high vegetation cover	↓ vegetation cover/↑ bare soil/ ↓ prey availability
Quiroga, 2004	Semi-arid Chaco (Arg)	Logging + grazing	nr	Constant	Species change/ grass herbivory	High tree cover/high litter cover	↓ tree/↑ shrub/↑ bare soil cover
Rodríguez, 2011	Central Monte (Arg)	Grazing	nr	Constant	Grass herbivory/ shrub redistribution	nr	nr
Simonetti, 1983	Matorral (Chile)	Grazing	Intense	Constant	Shrub defoliation/ grass herbivory	65.7% shrub cover/ 14.3% herbs cover	8.9% shrub cover/90.1% herbs cover
Tabeni and Ojeda, 2005	Central Monte (Arg)	Grazing	4–6.63 feces/1600 m ²	Constant	Grass herbivory/ shrub redistribution	Big size vegetation patches/ high veg. connectivity	↓ patch size/↑ bare soil connectivity/ ↓ grass cover
Valone and Sauter, 2005	Arizona (USA)	Grazing	nr	Constant	Grass herbivory/ shrub redistribution	±30% plant cover/25% shrub cover/5% grass cover	±22% plant cover/20% shrub cover/ 0% grass cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (2 yr.)	401 ha	nr	Species changes/ resource changes	26% annual/9% bunch-grasses/ 27% perennial cover	73% annual/1% bunch-grasses/ 1% perennial cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (9 yr.)	770 ha	nr	Species changes/ resource changes	20% annual cover/46% perennial cover	62% annual/8% bunch-grasses/ 13% perennial cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (13 yr.)	2234 ha	nr	Species changes/ resource changes	21% annual/3% bunch-grasses/ 37% perennial cover	19% annual/1% bunch-grasses/ 21% perennial cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (15 yr.)	38 ha	nr	Species changes/ resource changes	15% annual/3% bunch-grasses/ 40% perennial cover	7% annual/7% bunch-grasses/ 9% perennial cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (19 yr.)	10 ha	nr	Species changes/ resource changes	25% annual/6% bunch-grasses/ 28% perennial cover	34% annual/18% bunch-grasses/ 4% perennial cover
Vamstad and Rotenberry, 2010	Mojave (USA)	Old fire (65 yr.)	372 ha	nr	Species changes/ resource changes	28% annual/2% bunch-grasses/ 20% perennial cover	59% annual/25% bunch-grasses/ 2% perennial cover

Abbreviations are USA = United States of America, S.Africa = South Africa, Arg = Argentina, Aus = Australia, nr = not reported.

disturbances. Despite the fact that most of them showed no statistical significance, the observed negative pattern (i.e. diminished functional diversity under disturbance) was present in the majority of the case-studies analyzed. Furthermore, we found that the mean grand effect size was negative and significant, and that functional diversity responses vary accordingly to the mechanism by which the disturbance affects the ecosystem.

There is an increasing evidence of the negative effect of anthropogenic drivers of disturbance over animal functional diversity. Ernst et al. (2006) reported a pronounced and significant decline in anuran functional diversity in logged tropical forests of two continents. They suggest that extinction followed a non-random pattern, being trait dependent, with the predisposition related to specific adaptations rather than trophically bias. Larsen et al. (2005) found that agricultural intensification disrupt ecosystem functioning through the extinction of pollinators, being large-bodied species the most functionally efficient but also the most extinction-prone. Also under agricultural intensification, Flynn et al. (2009) detected that birds and mammals functional diversity was more intensively affected than plants functional diversity. Moreover, they found that species loss is not random, and that functionally unique species may be lost more quickly than those functionally redundant. Our results are the first to show that human-induced disturbances reduce animal functional diversity in arid lands biomes; this is about 40% of land surface of the world (Reynolds et al., 2007). Moreover, arid lands mammals are adapted to strong environmental constraints and present a wide diversity of endemism (Mares, 1992), and here we showed that disturbance diminish the diversity of resource use traits of mammal assemblages. Thus conservation concern of arid lands mammals should rise if extinction risk is predisposing to habitat adaptations (Ernst et al., 2006).

It has been suggested that species segregates in space traits with sufficient dimensions and very little (if any) redundancy of species contribution is possible when considering ecosystem multifunctionality (Hector and Bagchi, 2007; Petchey and Gaston, 2002). Data for our traits was collected from publications and available information rather than directly measured (i.e. 'hard' vs. 'soft' traits, Cornelissen et al., 2003). The use of these coarse traits may have diminished our ability to detect unique-trait species, and may be one of the reasons of the low significance of the heterogeneity test results. Moreover, we should expect that finer resolution in trait data would enhance the power of the statistical analysis and our capacity to identify more subtle changes. However, the lack of published detailed functional traits (i.e. percentage of consumed items in diets) would have not allowed us to include all the species that were considered in this analysis. Nevertheless, our results show a significant decrease of the functional traits related to the processing of matter and energy, and point toward some of the factors involved in the desertification process (Duffy, 2003; Schlesinger et al., 1990). Thus, the loss of mammal functional diversity may generate positive feedbacks that help to maintain undesired degraded states of the ecosystem (i.e. desertification).

Other taxa may be redundant in the functional trait space that mammals occupy and potentially buffer the negative effect of human-induced disturbance (i.e. granivorous birds, social ground-dwelling insects). This possibility of functional redundancy and complementarity among taxa and their response to disturbances is beyond the scope of this paper and needs to be explored in detail; in particular because of a potential insurance effect given by the diversity in responses to the disturbance (Chillo et al., 2011). However bird's trophic guilds are negatively affected by grazing and fire in arid lands (Marone, 1990; Milesi et al., 2002). Also, ant's functional richness and diversity are negatively affected by disturbance (Beever et al., 2003; Bestelmeyer and Wiens, 1996;

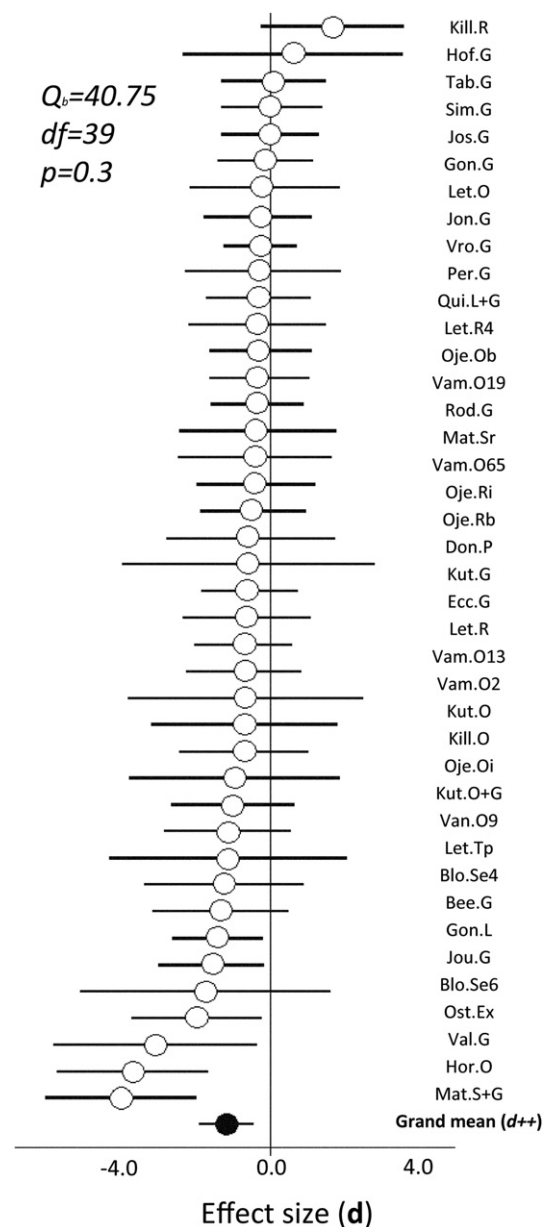


Fig. 1. Individual effect sizes and overall grand mean effect size (d_{++}) (Hedge's d), and 95% confidence intervals for the effect of disturbance on mammal's functional diversity. Names are the first letters of the first author of the reference and the capital letter are the type of disturbance (i.e. 'Kill.R' = Killgore et al., 2009; Recent fire. Appendix S1).

Hoffmann, 2010). As mammals, these taxa show similar functional diversity, and also respond negatively to disturbance in different ecosystems (Flynn et al., 2009; Karp et al., 2011).

The effects of disturbance driven by human activities on ecosystem are highly complex due to differences in intensity, distribution, amount, initial conditions and legacies. Here, we presented a disaggregated analysis of disturbance (Peters et al., 2011), which allowed us to better analyze mammal functional diversity response, based on the information that could be properly characterized. Mammal functional diversity in arid lands differs in the response to the mechanism by which disturbance affects ecosystem, more than to the specific type of disturbance. Our results show that 'herbivory' is the least aggressive effect over mammal functional diversity. This biotic mechanism effect implies mainly biomass removal (shrubs and grasses defoliation) by

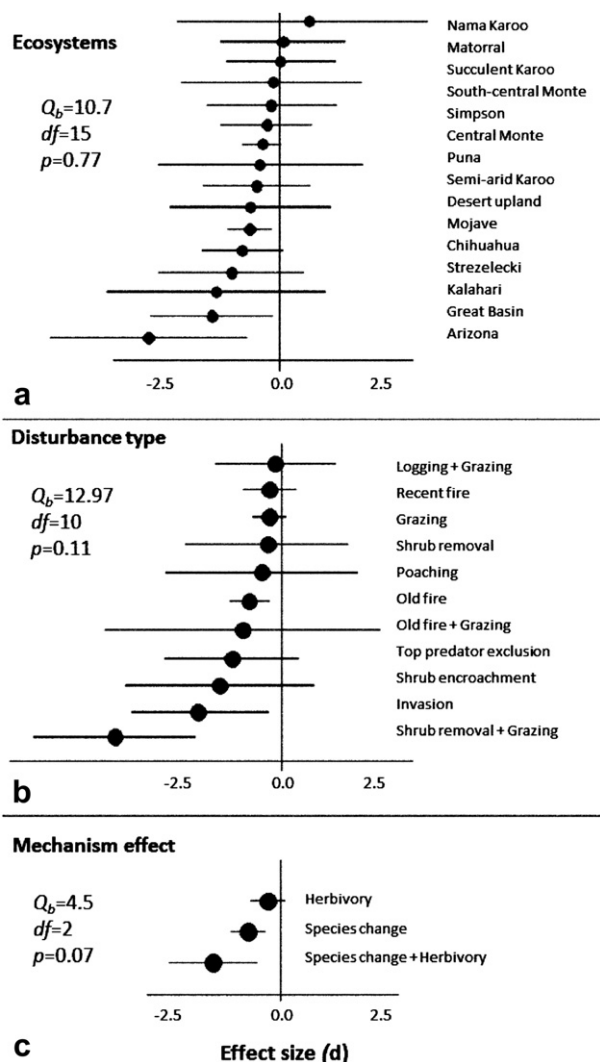


Fig. 2. Effect size (*d*) of mammal functional diversity grouped into three moderator factors: ecosystems (a), disturbance type (b) and mechanism effect (c); based on information presented in Table 2.

livestock (cows, goats, sheeps and/or horses), which we named after 'herbivory' in order to simplify the analysis. This affects mainly the structure and relative composition of vegetation and landscape heterogeneity. The fact that livestock production – constant and dominant in arid lands – does not represent the most aggressive human activity to mammal functional diversity should open new avenues of research and discussions regarding alternative management strategies of sustainable livestock production (Briske et al., 2008; Cingolani et al., 2008; Reynolds et al., 2007).

On the contrary, our concern is with regard to human activities which generate new ecosystem states given by vegetation species and resource changes; as we found 'species change' (i.e. vegetation changes in this paper) mechanism effect to be significantly negative to mammal functional diversity. This mechanism effect is attributable to a change in initial state properties, and even sometimes to the outcome of a new state after years without disturbance. For example, when comparing between disturbance types, 'old fire' had a stronger negative effect over mammal functional diversity than 'recent fire'. Surprisingly, our results show that the elimination of vegetation structure does not represent as big change as the replacement for new type of vegetation composition and structure. Thus, these ecological impacts of changing resource availability demonstrated to be

a stronger determinant to mammal functional diversity decline. Disturbances such as shrub encroachment/elimination and species invasion/elimination intuitively seem to have opposite outcomes (at least in vegetation structure), but our results show that the effect over mammal functional diversity is the same. The occurrence of new states due to disturbances that changes the trajectory of the system is known to generate catastrophic regime shifts in ecosystems dynamic (Scheffer and Carpenter, 2003). Here we show that when disturbance generates changes in plant species and resources and in initial state properties, the regime shift seen in vegetation have drastic consequences over mammal functional diversity. Unfortunately, as some studies do not report the initial and final state properties we could not generalize the analysis, and this should be a research priority in future studies.

Disturbance effect over biodiversity may be as complex as disturbance *per se*, highly dependable of ecosystem initial conditions and species life histories (Cingolani et al., 2008; Mackey and Currie, 2001; Tabeni and Ojeda, 2003). Moreover, it is well known that diversity contributes to maintaining ecosystem functioning, and that ecosystem functions are a top conservation priority because human survival depends on the services they provide (Chapin et al., 2000; Hector and Bagchi, 2007). Worldwide, these services range from storing carbon to producing food; and in particular nutrient cycling is a baseline process involved in food production and seriously threatens by desertification in arid lands (Millennium Ecosystem Assessment, 2005).

Conserving mammal functional diversity may help to avoid positive feedbacks that maintain degraded states of the ecosystem, by improving resource use and distribution. As the contribution of different species vary widely in regards of matter and energy flow, conservation efforts should focus on traits and functional diversity (Cadotte, 2011). In conclusion, our results pinpoint on the mechanisms by which different types of disturbances in arid lands affect mammal functional diversity, and suggest that conservation should focus on avoiding drastic changes in ecosystem properties. These significant changes in vegetation composition and structure drive significant losses in functional diversity, and consequently altering ecosystem trajectory.

Acknowledgments

We thank P. Sassi, L.C.R. Silva, S. Albanese, M.E. Periago and M.D. Rodríguez for useful discussions of ideas and suggestions on early drafts; two anonymous Reviewers help to improve the manuscript; R. Aguilar and R. Ovejero helped with meta-analysis. This project was partially financed by CONICET (PIP-5944) and Agencia (PICT-25778; 0455).

Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jaridenv.2012.06.016>.

References

Bardgett, R.D., Wardle, D., 2003. Herbivore-mediated linkages between above-ground and belowground communities. *Ecology* 84, 2258–2268.
 Beaver, E.A., Tausch, R.J., Brussard, P.F., 2003. Characterizing grazing disturbance in semiarid ecosystems across broad scales, using diversity indices. *Ecological Applications* 13, 119–136.
 Bertiller, M.B., Marone, L., Baldi, R., Ares, J.O., 2009. Biological interactions at different spatial scales in the Monte desert of Argentina. *Journal of Arid Environments* 73, 212–221.
 Bestelmeyer, T.B., Wiens, J.A., 1996. The effect of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* 6, 1225–1240.

- Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16, 533–540.
- Briske, D.D., Bestelmeyer, B.T., Stringham, T.K., Shaver, P.L., 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology and Management* 61, 359–367.
- Cadotte, M.W., 2011. The new diversity: management gains through insights into the functional diversity of communities. *Journal of Applied Ecology* 48, 1067–1069.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443, 989–992.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Taylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.V., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Chillo, V., Anand, M., Ojeda, R.A., 2011. Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems* 14, 1168–1177.
- Cingolani, A.M., Noy-Meir, I., Renison, D.D., Cabido, M., 2008. La ganadería extensiva, ¿es compatible con la conservación de la biodiversidad y de los suelos? *Ecología Austral* 18, 253–271.
- Cornelissen, A.J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51, 335–380.
- Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16, 646–655.
- Duffy, J.E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6, 680–687.
- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E., Loreau, M., 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10, 522–538.
- Ernst, R., Linsenmair, K.E., Rödel, M.O., 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biological Conservation* 133, 143–155.
- Flynn, D.F.B., Gogol-Prokurat, T., Molinari, N., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12, 22–33.
- Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analysis. *Ecology* 80, 1142–1149.
- Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448, 188–191.
- Hedges, L.V., Olkin, I., 1985. *Statistical Methods for Meta-Analysis*. Academic Press, New York.
- Hoffmann, B.D., 2010. Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing. *Ecological Indicators* 10, 105–111.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
- Karp, D.S., Ziv, G., Zook, J., Ehrlich, P.R., Daily, G.C., 2011. Resilience and stability in bird guilds across tropical countryside. *PNAS* 108, 21134–21139.
- Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8, 538–547.
- Loreau, M., Naeem, S., Inchausti, P., 2002. *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, New York.
- Mackey, R.L., Currie, D.J., 2001. The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492.
- Mares, M.A., 1992. Neotropical mammals and the myth of Amazonian biodiversity. *Science* 255, 976–979.
- Marone, L., 1990. Modifications of local and regional bird diversity after a fire in the Monte desert, Argentina. *Revista Chilena de Historia Natural* 63, 187–195.
- Milesi, F.A., Marone, L., Lopez De Casenave, J., Cueto, V., Mezquida, E.T., 2002. Gremios de manejo como indicadores de las condiciones del ambiente: un estudio de caso con aves y perturbaciones del hábitat en el Monte central, Argentina. *Ecología Austral* 12, 149–161.
- Millennium Ecosystem Assessment, 2005. *Synthesis Reports*. www.maweb.org.
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Moullot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24, 867–876.
- Noy-Meir, I., 1974. Desert ecosystems: higher trophic levels. *Annual Review of Ecology and Systematics* 5, 195–214.
- Noy-Meir, I., 1979. Structure and function of desert ecosystem. *Israel Journal of Botany* 28, 1–19.
- Petchey, O.L., Gaston, K.J., 2002. Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London* 269, 1721–1727.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9, 741–758.
- Peters, D.P.C., Lugo, A.E., Chapin III, S.F., Pickett, S.T.A., Duniway, M., Rocha, A.V., Swanson, F.J., Laney, C., Jones, J., 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2, 1–26.
- Polis, G.A., 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *The American Naturalist* 138, 123–155.
- Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. *Science* 316, 847–851.
- Rosenberg, M.S., Adams, D.C., Gurevitch, J., 2000. *MetaWin: Statistical Software for Meta-Analysis, Version 2.0*. Sinauer Associated Inc., Sunderland, MA.
- Scheffer, M., Carpenter, S., 2003. Catastrophic regime shifts in ecosystems: linking theory with observation. *Trends in Ecology and Evolution* 18, 648–656.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. *Science* 247, 1043–1048.
- Shachak, M., Gosz, J.R., Pickett, S.T.A., Perevolotsky, A., 2005. *Biodiversity in Drylands: Toward a Unified Framework*. Oxford University Press, New York.
- Tabeni, S., Ojeda, R.A., 2003. Assessing mammal responses to perturbations in temperate aridlands of Argentina. *Journal of Arid Environments* 55, 715–726.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2002. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–854.
- Walker, B., Kinzig, A., Langridge, J., 1999. Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, USA.
- Whitford, W., 2002. *Ecology of Desert Systems*. Academic Press. Elsevier Science Imprint, London.