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Animal feedbacks in desertification: an overview

Actividad animal y desertificación: una visión general

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ABSTRACT

The role of animals as producers of patches that increase heterogeneity of soil resources is examined in relation to a conceptual model of desertification that focuses on change in relative homogeneity or heterogeneity in soil resources as the primary process in desertification. Examples of animal produced soil parches in the Chihuahuan Desert in North America include relatively large, persistent, nutrient enriched mounds of the large heteromyid rodent (*Dipodomys spectabilis*), cache pits produced by seed eating rodents, nests of seed harvesting ants and nests of other ant species. Desertification has resulted in changes in densities and species composition of animals that produce soil patches. Animal produced soil patches frequently differ in chemical composition and physical properties that affect water and nutrient availability. The spatial distribution of animal produced soil patches contributes to the concentration of resources in the shrub "islands" that characterize much of the desertified landscape in the Chihuahuan Desert. Examples of animal produced soil patches in other semi-arid ecosystems are discussed in relation to their potential feedbacks in the desertification process.

Key words: Animal effects, desertification, nitrogen mineralization, soil heterogeneity, soil nutrients, resource patches.

RESUMEN

El papel de los animales como productores de parches de recursos que incrementan la heterogeneidad del suelo es examinada en relación a un modelo conceptual de desertificación, que considera la relativa homogeneidad o heterogeneidad de los recursos del suelo como el primer paso en la desertificación. Ejemplos de parches de heterogeneidad de recursos en el suelo por inducción de animales incluye incrementos de nutrientes relativamente grandes y persistentes y enriquecidos con nutrientes producidos por el roedor heteromido *Dipodomys spectabilis*, hoyos producidos por los roedores granívoros, así como nidos de hormigas granívoras y de otras especies. La desertificación ha producido cambios en la densidad y composición de las especies animales que producen parches en el suelo. Los parches del suelo producidos por animales frecuentemente difieren en su composición química y propiedades físicas que afectan la disponibilidad de agua y nutrientes. La distribución espacial de parches del suelo producidos por animales contribuyen a la concentración de recursos en las "islas" de arbustos que caracterizan el paisaje desértico. Ejemplos de animales que producen manchas de recursos en suelos de los ecosistemas semiáridos son discutidos en relación a su retroalimentación potencial en el proceso de desertificación.

Palabras claves: Efectos animales, desertificación, mineralización de nitrógeno, heterogeneidad del suelo, nutrientes del suelo, parches de recursos.

INTRODUCTION

The United Nations defined desertification as: "the diminution or destruction of the biological of the land that can lead ultimately to desert-like conditions. It is an aspect of the widespread potential deterioration of ecosystems under the combined pressure of adverse and fluctuating climate and excessive exploitation. Such pressure has diminished or destroyed the biological potential, i.e., plant and animal production, for multiple use purposes at a time when increased productivity is needed to support growing populations in quest of development" (Vestraete 1983). This definition emphasizes the reduced biological potential of desertified ecosystems, but the paper in which this definition appeared and most other publications, on the subject do not focus on the functional and/or structural properties of the ecosystems undergoing desertification or of the desertified end points. An understanding of the functional and structural properties of such ecosystems in necessary if there is to be

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any possibility of halting and/or reversing the process and of managing desertified ecosystems in a sustainable and productive manner. The trend globally is for the degraded-desertified ecosystems to be even further degraded as the human inhabitants attempt to maximize harvestable yields from these ecosystems.

The focus of the Jornada Long Term Ecological Research Program in North America is on the processes that have led to the desertification of northern Chihuahuan Desert ecosystems and the structural and functional properties of these desertified ecosystems. The conceptual model upon which that program is based has been described in Schlesinger *et al.* (1990). They suggest that "changes in ecosystem function at the transition between arid and semi-arid regions are best understood in the context of the spatial and temporal distribution of soil resources." In the desert grasslands of North America a relatively homogeneous distribution of soil resources has been replaced by a spatially and temporally heterogeneous distribution of soil resources during the process of establishment of non-palatable woody shrubs and reduction in grass cover. The Jornada conceptual model (Fig. 1) was developed on the basis of studies in the Jornada Basin in southern New Mexico. Schlesinger *et al.* (1990) "believe that this model applies to desertification in other parts of the globe."

The generality of the Jornada desertification model must be tested on other desert margin areas of the world. The generality of this model may be questioned in terms of its applicability to the semi-arid region south of the Atacama in Chile where desertification may have increased the homogeneity of soil resources instead of increasing heterogeneity. If that is indeed the case, the conceptual model can be changed to a more general statement such as: desertification results in changes in spatial and temporal variability of soil resources, without specifing the direction of change. Such a change would only serve to generalize the Jornada model.

Schlesinger *et al.* (1990) concentrated their discussion of desertification on climatic effects, erosional processes and soil nutrient distributions. In addition to these abiotic driving forces that affect the spatial and temporal distribution of soil resources, there are important biotic processes that affect the relative homogeneity of soil resources. There are feedbacks between physical forces and biological activity that are operative during the degradation process and continue to operate in the desertified ecosystem. It is important to recognize these interactions and understand how they affect soil resources.

Although only a small fraction of the live biomass is consumed by animals, the importance of animals as agents affecting the structure, properties, and processes of ecosystems must be evaluated (Chew 1974). Restated, it is essential to examine the functional role of animals in ecosystems rather than to merely concentrate on animals as consumers of primary production. Animals affect soil structural and chemical properties in a variety of ways. In the progression of the desertification process, populations of some species decline, some disappear while others flourish in the "degraded" ecosystem. The shifts in composition on the animal communities have an effect not only on the structure but also the properties and functioning of the resulting ecosystems. This is especially true of animal species that have effects on soil properties and on the degree of heterogeneity of soils. These relationships may best be illustrated by some specific examples.

Effects of small mammals

In the northern Chihuahuan Desert of North America shrublands have replaced perennial grassland over most of the region. One inhabitat of the perennial grasslands, the banner-tailed kangaroo rat (*Dipodomys spectabilis*), does not survive in open shrublands. Despite the disappearance of this animal, the huge burrow systems (1-2 meters in diameter) that were occupied by successive generations of this species remain as distiguishable features in the shrub dominated ecosystems. In a study of *Larrea tridentata* dominated ecosystems in southeastern Arizona, *L. tridentata* exhibited die-back over most of the area except for those shrubs that were growing on the periphery of the *D. spectabilis* mounds (Chew & Whitford 1992). Although the mounds had not been occupied by *D. spectabilis* for more than 30 years, the mound soils were deeper, more friable, had elevated water content, and ex-

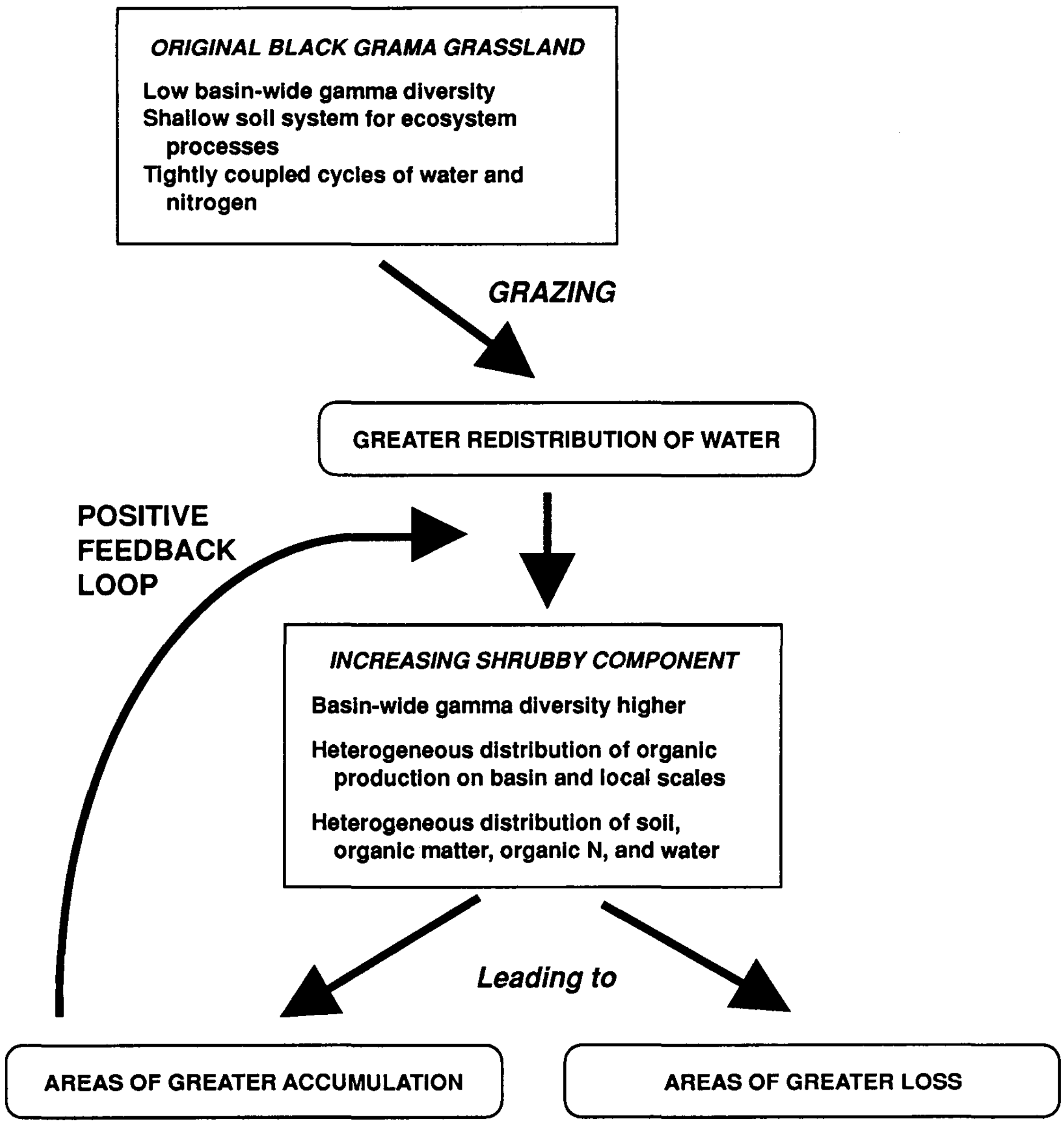

Fig. 1: A conceptual model of the desertification process in the northern Chihuahuan Desert (based on Schlesinger *et al.* 1990).

Modelo conceptual del proceso de desertificación en el norte del Desierto de Chihuahua (basado en Schlesinger *et al.* 1990).

hibited higher nitrogen mineralization potential rates and higher soil nitrogen than the surrounding soils (Chew & Whitford 1992) (Table 1). In other studies of *D. spectabilis* mounds in grassland ecosystems, the mound soils were also found to have higher nitrogen availability, higher nitrogen mineralization potentials, lower bulk density and higher water storage than non mound soils (Moorhead *et al.* 1988, Mun & Whitford 1990). In addition, *D. spectabilis* mounds supported a different ephemeral vegetation than was present in adjacent undisturbed areas (Moroka *et al.* 1982, Moorhead *et al.* 1988, Mun & Whitford 1990) (Table 2). Many of the ephemeral plants that dominate the *D. spectabilis* mounds are species that Gutiérrez & Whitford (1987) and Gutiérrez *et al.* (1988) found to be favored in

TABLE 1

A comparison of nitrogen mineralization and soil water content on banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds and areas off mounds. Water content data are for 8 cm depth cores. Data from Chew & Whitford 1992

Comparación entre la mineralización de nitrógeno y contenido de agua del suelo en montículos de la rata canguru (*Dipodomys spectabilis*) y fuera de ellos. Los datos de contenido de agua son de muestras de 8 cm de profundidad. Datos de Chew & Whitford 1992

	Mound	Off Mound
N Mineralization (mg/kg)	38.4	29.3
Water content (g/cm)		
Aug 5	7.9	3.8
Aug 14	5.6	3.3
Aug 23	6.3	3.5

TABLE 2

Comparison of biomass (g/m^2) of selected annual plants growing on banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds (M) and areas 3 m distance from mounds (O)

Comparación de biomasa (g/m^2) de plantas anuales seleccionadas creciendo en los montículos (M) de la rata canguru (*Dipodomys spectabilis*) y áreas a 3 m de distancia de los montículos (O)

	Spring Annuals	
	M	O
Descurainia pinnata	54.4	1.0
Lesquerella gordoni	45.7	12.0
Eschscholtzia mexicana	16.8	0.4
Eriastrum difussum	0.1	3.9
Summer Annuals		
Tidestromia lanuginosa	129.4	1.8
Boerhaavia spicata	10.2	0.9
Haplopappus gracilis	0.4	34.5

nitrogen rich soils. Thus the *D. spectabilis* mounds are an example of an animal produced patch that persists long after the local extinction of the species that produced the patch initially. The presence of such a patch in a desertified ecosystem may be an essential structure that allows certain plant species to remain as part of the desertified system. Despite the relative persistence of banner-tailed kangaroo rat mounds in desertified ecosystems, eventually these mounds will collapse and the elevated soil nutrients will be dispersed. Considering the dependence of selected species of plants on the nutrient rich mounds, as the mounds degrade such species will become increasingly rare in the ecosystem.

Animals may have effects on ecosystems that accelerate change or contribute to the maintenance of a system in an altered but relatively stable state. In the northern Chihuahuan Desert, the species richness and population densities of heteromyid rodents are higher in shrubland ecosystems than in the perennial grassland ecosystems. The heteromyid rodents dig numerous small pits in search of buried seeds and/or in the excavation of seed caches. The open pits are soon filled with wind transported plant litter and seeds and eventually covered with wind blown soil. The seeds that are accumulated in the pits are buried with a supply of organic matter that when decomposed produces a nutrient rich microsite. These cache pits are not randomly distributed. Densities of pits are high under the shrub canopies im shrubland ecosystems ($\bar{x}$ = 4.5 pits/m^2) whereas in open areas the average density is 0.08/m^2. In *L. tridentata* communities the densities of such pits varied between 0 and 7/m^2 in a random sampling of the area (Steinberger & Whitford 1983). The rapid decomposition of the small quantities of organic matter buried in the pits (Urbaniak & Whitford 1983) adds to the nutrient enrichment of the soils under shrub canopies. Such pits contribute to the "fertile island" characteristics of shrubs in this system (García-Moya & McKell 1970, Barth & Klemmedson 1978, Parker *et al.* 1982, Virginia & Jarrell 1983). It was calculated that 2 mg of nitrogen was made available by the decomposition of the litter in an average pit of 22 cm^2 surface area (Steinberger & Whitford 1983). This nitrogen adds to the "fertile island" phenomenon which enhances the capacity of these shrublands to resist perturbation and contributes to the stability of the desertified ecosystem.

There are a variety of animals that produce pits which act as seed and litter traps. The pists may be small in size and persist for a short period of time such as the rodent cache pits described above, or be large and persist for more than a year such as porcupine digs (Alkon & Olsvig-Whittaker 1989) and badger excavations (pers. obs.). The realtive contribution of a consumer species that produces soil pits to the desertification process and/or to the resistance or resilience of a desertified systems is not a function of the species but rather how the populations of that species are affected by shifts in the compositions and structure of the vegetation as a result of the disturbance. Those species that are able to thrive in the altered ecosystem will continue to contribute to the heterogeneity of the soil resources while other species may become locally extinct and their contribution to heterogeneity will be lost.

Effects of social insects

Desertification affects invertebrates as well as the vertebrate populations. In the Chichuahuan Desert two groups of arthropods (termites and ants) have been shown to have important effects on soil properties. Subterranean termites are major consumers of dead plant material (Whitford 1991) and greatly influence rainfall infiltration and soil water storage (Elkins *et al.* 1986, Whitford 1991). The degree to which desertification affects termite populations depends upon the dietary breadth of the species and the degree of change in the vegetation. For example, the dominant termite species in the northern Chihuahuan Desert, *Gnathamitermes tubiformans*, is an extreme food generalist and its populations appear not to have been affected by the shift from grassland to shrub dominated ecosystems (Whitford 1991). Thus it is not likely that there are any positive or negative feedbacks on desertification by these insects in those ecosystems.

Most arid regions of the world support a diverse and abundant ant fauna. Ants modify soil properties by their habit of building subterranean nests and accumulating unconsumed food in the nest chambers or around the nest disc in refuse piles. Ant nests affect the macroporosity of the soil thereby increasing infiltration. The effects of ant nests on infiltration have been documented in a number of papers (Lobry de Bruyn & Conacher 1990). In addition to the hydrological effect of ant nests, the area around the nest disc of some species may be nutrient enriched (Lobry de Bruyn & Conacher 1990). Changes in vegetation and soil have dramatic effects on the species composition and colony densities of ants in semiarid ecosystems.

The probable consequences of desertification on ecosystem properties and processes resulting from shifts in the ant fauna may be elucidated by examining the changes in the ant communities of areas exhibiting varying degrees of degradation. In the basin grassland on the Jornada in southern New Mexico, the distribution of harvester ants is patchy. In some areas *Pogonomyrmex desertorum* is the only large seed harvesting ant present (Table 3). This species constructs relatively small nests that produce no detectable nutrient enriched halo zone around the nest. The primary effect of this species on soil properties is limited to that of nest tunnels and galleries on soil macroporosity. In other grasslands, the large harvester ant, *Pogonomyrmex rugosus* occurs in varying densities (Table 3). The persistent nests of this species have been shown to produce nutrient enrichment around the nest disc in some but not all locations (Whitford 1988, DiMarco 1987). However there is considerable variation in the degree of nutrient enrichment and the kinds of nutrients that are accumulated in the nest disc perimeter (Table 4). The nutrient enriched nest disc perimeters produce patches of vegetation that differ from the surrounding areas (DiMarco 1987) and the species composition of this plant assemblage differs among areas. The change from perennial grassland to mesquite (*Prosopis glandulosa*) dune ecosystems has resulted in a marked shift in the ant species and their distributions (Wisdom & Whitford 1981). They reported that in the mesquite dune habitat, fungus culturing ants, *Trachymyrmex smithii neomexicanus*, occupied dune flanks. These ants were not present in the grassland sites sampled by Wisdom & Whitford (1981).

The conversion of the basin grassland to mesquite dune landscapes has been accompanied by major changes in ant species composition (Table 3). The abundance of honey pot ants (*Myrmecocystus depilis*) is considerably greater in the mesquite dunes and one

TABLE 3

Comparison of densities of colonies of selected ant species in remnant grassland habitats and habitats that were grassland in the 1850's and that exhibit varying degrees of desertification on the Jornada Range in southern New Mexico. *Indicates slight desertification. **Indicates moderate desertification. ***Indicates severe desertification

Comparación de densidades de colonias de especies de hormigas seleccionadas en hábitat de pastizales remanentes y hábitat que fueron pastizales en 1850's y que exhiben diversos grados de desertificación en el campo experimental Jornada Range en el sur de Nuevo México. *Indica desertificación leve. **Indica desertificación moderada. ***Indica desertificación severa

Species	Creosotebush (*Larrea*) habitats 1***	2***	3***	Tarbush (*Flourensia*) habitats 1***	2***	3***
Pogonomyrmex desertorum	6.1	0	0	0	0	4.0
Pogonomyrmex rugosus	0	0	0	2.0	0	0
Novomessor cockerelli	0	4.0	2.0	6.1	0	0
Pheidole spp.	4.0	2.0	6.0	0	24.2	11.2
Myrmecocystus depilis	10.2	12.2	14.8	10.2	4.0	20.4
Myrmecocystus mexicanus	2.0	4.0	2.0	0	2.0	2.0
Trachymyrmex smithii	0	0	0	0	0	0

1 Larrea 1 m height, sand
2 Larrea 0.5 m height, gravel
3 Larrea 0.3 m height, caliche

1 Tarbush, burrograss
2 Tarbush, basin open
3 Tarbush, bunch grasses

Species	Grassland (*Bouteloua sporobolus*) habitats 1**	2*	3*	Mesquite (*Prosopis*) habitats 1**	2**	3***
Pogonomyrmex desertorum	4.0	2.0	38.9	4.0	0	4.0
Pogonomyrmex rugosus	8.1	4.0	0	0	0	0
Novomessor cockerelli	6.1	0	0	0	0	0
Pheidole spp.	0	0	6.1	0	0	0
Myrmecocystus depilis	2.0	0	0	14.8	8.1	10.2
Myrmecocystus mexicanus	0	0	0	0	0	0
Trachymyrmex smithii	0	0	0	2.0	2.0	12.2

1 Base of watershed
2 Mountain piedmont
3 Basin grassland

1 Incipient dunes
2 small dunes < 1 m height
3 Large dunes > 1 m height

species of fungus culturing ant (*Trachymyrmex smithii*) that does not occur in any of the grassland habitats is a dominant ant species in the mesquite dunefield ecosystem. Honey pot ants (*Myrmecocystus* spp.), collect honey dew from Homopterans and also consume small quantities of insects. Thus, soils surrounding their nests are not enriched by materials stored in surface galleries nor by non-edible materials rejected by the ants and accumulated in chaff piles near the nest entrance. However, the construction of nest caps with materials transported to the surface from depths > 1 m changes the chemical composition of the nest cap and its immediate environs (Table 5). Nests of *Trachymyrmex smithii* in mesquite dune habitats are also characterized by cemented nest caps that add large quantities of calcium carbonate to the soils around their nests. *T. smithii* colonies also modify soil properties by culturing fungi on macerated mesquite (*Prosopis glandulosa*), leaves. Over time these nests may become organically rich microsites in the dune ecosystem. At the present time, the only detectable soil differences are the result of materials transported to the surface to construct the cemented caps.

in certain sand dune habitats, a species of seed harvesting ant (*Pogonomyrmex maricopa*) that is absent in grasslands is the dominant ant species. These ants construct deep nests and cement the caps that cover the surficial chambers with calcium carbonate. These caps are produced during the wet season and resist

TABLE 4

The effects of nests of harvester ants, *Pogonomyrmex rugosus* on selected soil chemical properties in three locations on a Chihuahuan Desert watershed. Concentrations are Ca^{++} and Mg^{++} in meq/100 g soil; NO_3-N, NH_4, -N, Total N and inorganic P in mg/kg soil. AN indicates samples from nest perimeter, OAN indicates samples 5 m from the nest edge, * $P < 0.05$, ** $P < 0.01$, data from DiMarco (1987)

Efecto de los nidos de las hormigas cosechadoras (*Pogonomyrmex rugosus*) en propiedades químicas del suelo, seleccionadas en tres localidades de la cuenca del desierto chihuahuense. Las concentraciones de Ca^{++} y Mg^{++} son expresadas en meq/100 g del suelo; NO_3-N, NH_4, -N, nitrógeno total y fósforo inorgánico en mg/kg de suelo. AN indica muestras en el perímetro del nido, OAN indica muestras a 5 m de la orilla del nido, * P < 0,05, ** P < 0,01, datos obtenidos de DiMarco (1987)

Chemical Property	*Scleropogon-Hilaria* basin grassland		Mixed shrubland lower slope		Sub-shrub grassland mid-slope	
	AN	OAN	AN	OAN	AN	OAN
Calcium	21.8	24.8 *	13.8	15.1	5.9	7.4
Magnesium	2.5	3.0 **	1.6	1.6	2.0	2.0
NO_3-N	8.2	2.6 **	1.8	0.8	2.5	0.8
NH_4-N	1.0	1.3	0.6	1.0	1.7	0.7 *
Total N	692.0	657.4 **	479.0	465.2	432.7	388.8 **
Inorganic P	12.4	7.4	4.7	4.6	20.4	8.0 **

TABLE 5

Concentrations (mg/kg soil) of selected cations and electrical conductivity in cemented ant nest caps and in adjacents soils. Numbers in parenthesis are standard desviations. *Significantly different from adjacent soils $P < 0.05$

Concentración (mg/kg de suelo) de algunos cationes seleccionados y conductividad eléctrica en tapas cementadas de nidos de hormigas y en suelos adyacentes. Los números en paréntesis son las desviaciones estándar. *Diferencia significativa entre suelos adyacentes P < 0,05

	Nest Cap	Adjacent
Calcium	1078 (725) *	62 (22.5)
Manganese	3.6 (0.66) *	1.2 (0.14)
Zinc	0.30 (0.13)	0.20 (0.02)
Copper	0.90 (0.11)	0.70 (0.12)
Iron	0.94 (0.14)	1.4 (0.66)
Sodium	7.4 (3.7)	12.2 (3.0)
Electrical conductivity (M ohms)	0.85 (0.40) *	0.06 (0.05)

erosion by wind blown sand during the spring windy season. At the beginning of the growing season when the deep soils are at temperatures below the optimum for growth and development, pupae and larvae are transported to the surficial chambers where they are exposed to higher temperatures. The nest caps are eroded away during the spring and early summer thus contributing cations and calcium carbonate to surrounding soils. The eroded caps are rebuilt each year during the wet season.

These examples from North American ecosystems that have experienced varying degres of desertification during the past one hundred and fifty years do not represent an exhaustive list of animal produced feedbacks in the desertification process, nor an exhaustive list of animal effects on the properties of desertified ecosystems. They do serve to illustrate how activities of animals that affect soil properties can modify the structure and functional properties of ecosystems that have been subjected to disturbance. Animals respond to disturbance by changing population densities and/or by local extinction or dominance. Because soil properties are to a large extent the determinants of the assemblages of organisms in an ecosystem, organisms that change those properties have marked effects on the properties and processes of the resulting ecosystems. In arid and semi-arid ecosystems, disturbance leading to landscapes recognized as desertified may be relatively rapid and the resultant ecosystems may be deemed to be relatively stable. However, the activities of the "new" assemblage of animals may produce slow changes in soil properties that eventually result in another incremental change in the structure of the already "desertified" ecosystem.

Animals and soil heterogeneity - examples from other regions

Animal activities similar to those reviewed above for the Chihuahuan Desert probably have effects on the properties and processes of ecosystems in other arid and semi-arid regions of the world. In studies in banded mulga ecosystems in northwestern New South Wales in Australia, we documented a number of patch generating activities of animals. Log mounds on erosion slopes in that system were permeated with termite galleries that undoubtedly contributed to the higher infiltration rates recorded for those mounds (Tongway *et al.* 1989). Subterranean termites produced a high density of storage galleries in a variety of ecosystems in the Australian arid zone (Whitford *et al.* 1992). In mulga groves, there are numerous ant colonies plus pits dug by *Varanus* spp. lizards. The presence of these soil disturbances in the mulga groves probably affects the water storage in the mulga band soils (Tongway & Ludwig 1990). In semi-arid regions in south Africa, large earth mounds, called heuweltjies by the local inhabitants, are persistent features of the lanscapes which occupy between 14 and 25% of the landscape (Lovegrove & Siegfried 1986, 1989). These mounds persist in agricultural areas even after having been plowed for at least 100 years. In untilled areas the mounds support and assemblage of plants that differs from surrounding areas thereby contributing to the heterogeneity of the ecosystem in which they occur.

In a recent study in the semi-arid zone of Chile, Contreras & Gutiérrez (1991) documented the effects of the soil digging activities of the subterranean rodent, *Spalacopus cyanus*, on the herbaceous vegetation. The total herbaceous biomas was 60% higher in areas with burrows of this animal.

These few examples of soil modifications by the activities of animals in other regions of the world are sufficient to suggest that the contribution of such animals to ecosystem properties and processes deserves more attention. Changes that are occurring in arid and semi-arid ecosystems today may be the result of local extinctions of animal species that played a key role in maintaining the heterogeneity or homogeneity of the ecosystems by their soil modification behavior. Until the full extent of such activities and their consequences are understood, it is doubtful that we will be able to halt or reverse the system changes that we call desertification.

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