THE PARADOX OF MESQUITES (*PROSOPIS* spp.): INVADING SPECIES OR BIODIVERSITY ENHANCERS?

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Resumen: Las zonas áridas y semiáridas presentan una gran diversidad de especies y están sujetas a un uso intenso, principalmente de ganadería extensiva. La expansión de las especies leñosas hacia los pastizales, conlleva un decremento en el valor de las tierras para ganadería pues se presenta la necesidad de controlar arbustos, lo que en el largo plazo no tiene buenos resultados. En este artículo se presenta una revisión bibliográfica de la importancia ecológica de las especies del género *Prosopis* (mezquites); se recopiló información de todas las especies asociadas a mezquite (ca. 208 géneros y alrededor de 660 especies de diversos taxa) y se propone la conservación de éstos para mantener la diversidad de las especies asociadas. Además, se resalta la importancia del mezquite como una especie clave para mantener el balance de nitrógeno y carbono en los suelos de las zonas áridas y semiáridas. Concluimos que la conservación de los mezquites debe tomarse en cuenta especialmente en las áreas en las que se pretende erradicarlo para introducir pastizales.

Palabras Clave: Zonas áridas, mezquites, manejo de pastizales, hábitat de fauna, incremento de leñosas.

Abstract. Arid and semi-arid environments contain relatively high species diversity and are subject to intense use, in particular extensive cattle grazing. The expansion of perennial species into the grasslands decreases the value of the rangeland, because it makes necessary to control the shrubs, which is not practical in the long term. This paper is a bibliographic review of the ecological importance of the *Prosopis* (mesquite) genus. We compiled information on all the species associated to mesquite (ca. 208 genera and 600 species from different taxa) and we propose that it is important to conserve the mesquites in order to maintain the diversity of the other associated species. We also stress the importance of mesquite as a keystone species in the balance of nitrogen and carbon in the arid and semiarid environments soils. We conclude that the conservation of the mesquites is very relevant, in particular in areas where people want to remove them and convert the environment to grasslands.

Key words: Arid environments, mesquites, rangeland management, wildlife habitat, encroachment of woody species.

Arid and semi-arid environments contain relatively high species diversity (Redford *et al.*, 1990) that decreases with increasing aridity (Huenneke and Noble, 1996). For example, the richest apifauna in the world is along the Mexico-USA border, with close to 900 species of solitary bees (Ayala *et al.*, 1993). Mexican xerophilous scrub and grasslands contain ca. 6 000 plant species (20% of total Mexican flora; Rzedowski, 1988) and Mexican desert scrub alone contains ca. 206 bird species (Escalante *et al.*, 1979). Biotic and abiotic resources in these environments are scarce and patchily distributed during most of the year, largely

depending on variable rainy periods (Noy-Meir, 1973). Spatial and temporal variation in rainfall, coupled with high average temperatures and differing soil textures, give rise to increased environmental heterogeneity which influences species diversity (Pianka, 1967; Rosenzweig and Winakur, 1969). Since environmental conditions are largely variable, net primary productivities are low (6 000-40 000 kg ha⁻¹) and the distribution and abundance of higher trophic levels are limited (Noy-Meir, 1973; Huenneke and Noble, 1996). Because of this relatively high species diversity, there is increasing concern on the conversion of

the arid environments that, for instance, may lead to desertification with a consequent loss of species diversity (Huenneke and Noble, 1996).

In particular, semi-arid grasslands and savannas of North America have recently undergone considerable change in structure and species composition (Buffington and Herbel, 1965). Especially, mesquite (*Prosopis* spp. L.) and juniper (*Juniperus occidentalis* Hook.) increase into southwestern savannas have had consequences on rangeland management. As a result, a wide array of research into the ecological impacts and control of encroaching species is being done. The increasing expansion of invading species has been attributed to a set of factors that range from drought, fire suppression, livestock grazing, and elevated atmospheric CO₂ concentrations (Archer *et al.*, 1988). Habitat fragmentation and livestock grazing of arid environments have had ecological costs, including disruption of ecosystem function, alteration of ecosystem structure and loss of species diversity (Aizen and Feinsinger, 1994a; 1994b; Fleischner, 1994; but see Brown, and MacDonald, 1995). We must therefore assess the relative importance of species interactions in these environments in order to quantify the ecological costs of fragmentation and conversion in order to propose management and conservation strategies. In this sense, we compile information on species that are associated with *Prosopis* spp. (mesquite) and point out its role in ecosystem functioning. We highlight the importance of mesquite for many species, and propose its conservation as a means of maintaining species diversity in arid environments.

Mesquite Biology

All species of mesquite (the genus *Prosopis*), comprising 10 species in North America (Rzedowski, 1988) and 28 species in South America (Burkhart, 1976), should be regarded as important ecologically for arid environments in the Americas. Mesquite are aggressive invaders (Glendening, 1952), due to the production of long-lived seeds that germinate in a wide range of edaphic conditions, rapid root growth and a high potential for N₂ fixation (Glendening, 1952; Polley *et al.*, 1994). However, mesquites have only recently expanded into grasslands from their characteristic mesic drainages and upland slopes, where they had been confined prior to livestock introductions during the Holocene (Polley *et al.*, 1994). Mesquites are common and often the dominant species of these arid and semiarid ecosystems, providing abundant resources at very specific times of the year (Simpson and Solbrig, 1977; Nilsen *et al.*, 1991). In South America and western USA, mesquites always bloom in spring

before the main rainy season (Simpson and Solbrig, 1977). In the southern Chihuahuan desert, during a three year period with widely varying precipitation (1994-1996; 138, 198.4 and 204.3 mm total annual rainfall, respectively), peak flowering periods in *Prosopis glandulosa* var. *torreyana* differed by less than ten days (Golubov, unpub. data). The phenological constancy of *Prosopis* species is in part due to a variety of adaptations to avoid water stress (e.g. phreatophytic root system, glabrous leaf surface, uncoupling of transpiration with atmospheric conditions, leaf size; Nilsen *et al.*, 1983), which permit an escape from temporal and spatial unpredictability of rainfall. This buffers mesquites against environmental stochasticity, allowing them to grow and to reproduce in the driest seasons, providing resources for organisms that feed on their nectar, pollen, leaves, bark and fruits (Simpson *et al.*, 1977).

Prosopis as a resource for animal and plant populations

Mesquites are used as a food, shelter and breeding area of a large number of invertebrate and vertebrate species (Table 1) having specific mutualistic interactions, such as those with solitary bees (e.g. *Perdita* spp.; Simpson *et al.*, 1977). In the southern Chihuahuan desert in March, *Prosopis glandulosa* and *Opuntia* spp. are the only dominant plants producing abundant flowers, pollen and nectar. While only 7 bee genera visit *Opuntia* spp. flowers (mostly oligolectic bees; Mandujano *et al.*, 1996), at least 20 genera visit *P. glandulosa* flowers (Lopez-Portillo *et al.*, 1993; Golubov *et al.*, 1999). Bird diversity has been shown to be higher in a *Prosopis juliflora* scrubland than in oak forests in western Mexico (Corcuera and Butterfield, 1999) and over 70 bird species are associated with mesquite scrublands in Mexico (Escalante *et al.*, 1979). Few examples have addressed the change in avian communities after mesquite removal (Soutiere and Boulén, 1976; Reitzel, 1982; Smith *et al.*, 1996; Nolte and Fulbright, 1997), but they all showed an increase in species diversity when mesquites were present when compared to grassland with no mesquites present. Reptile diversity and abundance has also shown to be higher in mesquite scrublands than in grasslands (Germano and Hungerford, 1981). Furthermore, mesquites are known to be visited by at least 200 species of herbivorous invertebrates (Cates and Rhoades, 1977; Wisdom, 1991) and by over 150 species of solitary bees (Simpson *et al.*, 1977). The habitat structure provided by areas with mesquites has been shown to influence arthropod diversity, mainly by providing architectural diversity (Gardner *et al.*, 1995). In addition, mes-

quites have important and often overlooked associations with nematodes (Freckman and Virginia, 1989) and symbiotic bacteria (Jenkins *et al.*, 1987).

Besides the animals that feed directly or indirectly on mesquites, a diverse flora can be found growing beneath them, including many cacti and grasses (Cornejo-Oviedo *et al.*, 1992; Suzan *et al.*, 1994; Mandujano *et al.* 1998). Thus, mesquites, as other perennial species of arid and semi-arid environments, may function as potential nurse plants by passive facilitation, providing nutrients such as carbon (C) and nitrogen (N), lower temperatures, higher humidity, and different microtopographies under their canopies

(Tiedeman and Klemmedson, 1973; Steenbergh and Lowe, 1977, Fulbright *et al.*, 1995). All of the above mentioned characteristics are pivotal in successional processes from savannas to mesquite thorn woodlands (Archer *et al.*, 1988). Given the high amount of interactions associated with *Prosopis* species, mesquites become ecologically important, especially providing a large amount of resources for many species.

Prosopis as a key element in ecosystems

At an ecosystem level, mesquites have been shown to have high net primary productivities (3,650 kg h⁻¹;

Table 1. Order, number of families, genera and species (in parenthesis) that use different resources of *Prosopis* spp. in arid environments. B = branches, BA = bark, F = fruits, L = leaves, N = nectar, P = pollen, M = microenvironment. Country abbreviations ARG = Argentina (Monte Desert and Chaco) MEX= Mexico (Chihuahuan and Sonoran Deserts), IND= India, USA= United States (Texas Plains, Sonoran and Chihuahuan Desert), AFR = Africa, MAG = Madagascar, IR = Iran, EG = Egypt.

Taxa	Fam	Genera	Resource	Source	Country where study conducted
Acari	3	24(?)	L	Wallwork <i>et al.</i> , 1985	USA
Angiosperms	24	48(69)	B, M	Mares <i>et al.</i> , 1977; McPherson <i>et al.</i> , 1988;	USA, ARG,
				Suzan <i>et al.</i> , 1994; Nabhan and Suzán, 1994; Franco-Pizaña <i>et al.</i> , 1995.	USA, ARG, IND, SA
Artiodactyla	2	3(4)	F, L	Mares <i>et al.</i> , 1977; Arnold and Dawe, 1979; Goyal <i>et al.</i> , 1988; Zimmerman 1991	
Coleoptera	8	44(72)	L, S, BA, S	Wallwork <i>et al.</i> , 1985; Wisdom, 1991; Ward, 1977.	USA, MEX, AFR, MAD, IND, IR
Diptera	1	1(1)	N, F	Keys <i>et al.</i> , 1995	USA
Hemiptera	8	31(40)	L	Wallwork <i>et al.</i> , 1985; Wisdom, 1991	USA, MEX
Homoptera	11	42(46)	L	Wisdom, 1991, Ward, 1977	USA, MEX, EG, IND
Hymenoptera	6	20(79)	P, N	Golubov <i>et al.</i> , 1999	MEX
Hymenoptera	?	?(160)	P, N	Simpson and Solbrig, 1977	USA, ARG
Lagomorpha	1	2(2)	B, F	Glendening, 1952; Mares <i>et al.</i> , 1977; Alipayou <i>et al.</i> , 1993	USA, ARG
Lepidoptera	10	18(20)	L, N	Wisdom, 1991; Rivera-García and Equihua-Zamora, 1997, Ward, 1977	USA, MEX, IND
Nematoda	?	5(?)	R	Freckman and Virginia, 1989	USA
Orthoptera	3	16(21)	L	Wisdom, 1991	USA, MEX
Reptilia	1	4(4)	M	Germano and Hungerford, 1981	USA
Rodentia	7	16(28)	S, B	Glendening, 1952; Rogovin and Surov, 1992; Rosati and Bucher, 1995	USA, MEX, ARG
Thysanoptera	2	2(2)	L, P, N	Wisdom, 1991	USA, MEX

Sharifi *et al.*, 1982) and, as other Leguminosae, are able to fix atmospheric nitrogen. This N_2 fixation is by means of nodulating rhizobia, that improve soil fertility at different depths (Jenkins *et al.*, 1987) and increases microbial biodiversity. Large amounts of N ($2,500 \text{ kg NO}_3\text{-N ha}^{-1}$) associated to litter decomposition outweighs denitrification processes under mesquite canopies (0.5 kg N ha^{-1} ; Virginia *et al.*, 1982, 1983). Given the scarcity of N in arid and semi-arid environments, the large amount of N fixed by *Prosopis* ($45\text{--}150 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) makes it a large contributor to the N budget of these environments (Johnson and Mayeux, 1990). The large amount of N found in mesquite "fertility islands" would suggest increases in shrub species growth associated to them. Barnes and Archer (1996) did not find a significant effect of a *Prosopis glandulosa* Torr. overstory on physiological characteristics and growth of 7 associated shrub species. In contrast, Tiedeman and Klemmedson (1973) showed that the Arizona cottontop (*Trichachne californica*) had 15 times greater N yields in mesquite soil although there was only a 3 fold difference in N between soils. Furthermore, there seems to exist some passive facilitation of *Prosopis* species towards other shrubs such as *Celtis* (Franco-Pizana *et al.*, 1995). Apparently, conditions for conversion of organic N to available forms are more favorable in soil under mesquite than in adjacent soil. Even compared to other leguminous shrubs of arid and semi-arid environments such as ironwood (*Olneya tesota*) N_2 fixation was higher under mesquite individuals (Shearer *et al.*, 1983).

In general, soil properties beneath mesquites have been shown to favor water infiltration, avoiding soil sealing after heavy rainfall (Virginia and Jarell, 1983) and their association with nematodes seems to be an important component of deep soil nutrient cycling (Freckman and Virginia, 1989). In addition, high annual litter to soil coupled with subsequent decomposition and a low leaching environment found under mesquite canopies provides an accumulation of CA^+ and Mg^{2+} (Virginia and Jarell, 1983). Shrub communities such as those associated to mesquite enhance spatial heterogeneity of soil resources and biomass (Connin *et al.*, in press) creating "islands of fertility". The change from surface to deep C storage by shrubs leads to a greater long-term C storage in soils. However not all shrubs act similarly, in particular, mesquite communities maintain total C levels while other shrubs such as the creosote bush (*Larrea tridentata*) have a net loss of soil C (Connin *et al.*, in press). The increase of atmospheric CO_2 concentration since the early 1800's has been said to have favored C_3 over C_4 plants, however, the loss of productive grasslands to shrublands appears to be unrelated to climatic fluctuations,

and the conversion of grasslands to scrublands is largely attributed to anthropogenic disturbances (Connin *et al.*, in press). At an ecosystem level mesquite dominated communities, by creating "islands of fertility" and enhancing environmental heterogeneity, provides an increase in species richness.

Management Practices

Mesquite encroachment to desert grasslands is partially due to inadequate management of arid environments and rangelands. Historically, the Sonoran and Chihuahuan Deserts were covered by a dry tropical forest in the late Eocene that has experienced a drying trend, especially in the last 8,000 years (Smeins, 1983). The expansion of shrublands has thus created an "impoverished" system for livestock grazing, which in turn has reduced the income of many rangelands. Mesquite is often associated to impoverished ranges as it gradually replaces desirable grasses, it increases soil erosion and higher water runoff, while it decreases soil nutrients, and increases environmental heterogeneity. The vast prairies observed by European settlers may in fact be remnants from previous favorable conditions for grasslands. These persisting grasslands in the already deteriorating environment have surely been accelerated with the intensity of livestock grazing. In relation to native Holocene fauna (rodents, peccary and coyote) livestock have become a much more effective disperser (Janzen, 1986; Brown and Archer, 1987), coupled with prolonged livestock grazing and high grazing intensities have caused the doubling of mesquite cover in grasslands (Glendenning, 1952; Buffington and Herbel, 1965). These rangelands have frequently been cleared in favor of introduced grass species that often affect ecosystem structure and functioning (Fleischner, 1994; Pierson and McAuliffe, 1994). Furthermore, clearing of mesquites does not result in long-term favorable responses of forage grasses (Holecheck *et al.*, 1994) and does not seem to decrease water evaporation (Dugas and Mayeux, 1991). Studies on how mesquite influences vegetation, show little effects on perennial grasses and non-poisonous forbs at mesquite cover levels below 17% (Warren *et al.*, 1996). Besides supporting a large number of animals, *Prosopis* spp. provide resources for a large variety of income producing game such as mule deer (*Odocoileus hemionus*), bobwhite quail (*Collinus virginianus*), collared peccary (*Tayassu tajacu*), mourning dove (*Zenaidura macroura*) and wild turkey (*Meleagris gallopavo*; Mares *et al.*, 1977; Germano *et al.*, 1983; Scifres *et al.*, 1988). Mesquites also provide favorable conditions for native herbaceous, ephemeral and perennial plants under their canopies that are palat-

able for both livestock and wildlife (such as the Texas wintergrass *Setaria texana*; Heitschmidt *et al.*, 1986, and *Panicum mexicanum*; Cornejo-Oviedo *et al.*, 1992; Nolte and Fulbright, 1997). In addition, mesquites are often used as multipurpose agroforestry species as they provide fodder, food, fuel, nitrogen fixation, dune stabilization, soil conservation and honey production (Nair *et al.*, 1984; Fagg and Stewart, 1994), as well as for the recovery of salt lands (Singh, 1995). It is therefore important to take into account the way brush management is seen, from "eradication" to brush "management". Mesquite problems arise in grassland areas and regions where they were introduced for agroforestry. Many indigenous cultures and local communities in Argentina and the southern semi-arid environments of Mexico depend on mesquite where *Prosopis* is used for livestock forage, food, shade and fuel (D'Antoni and Solbrig, 1977).

The question arises as to the proper balance between conservation and exploitation of rangelands. Studies in the South American Chaco have shown a negative effect of fragmentation on bee pollinators and on reproduction of several arid and semi-arid zone plant species (Aizen and Feinsinger, 1994a; 1994b). Bock *et al.* (1993) suggested the exclusion of livestock from 20% of current federal grazing lands and Scifres *et al.* (1983) suggested creating mosaics of mesquite infested fields, which could enhance diversity (Whittaker *et al.*, 1979), however, mesquite stands will eventually coalesce into larger thorn woodlands (Archer *et al.*, 1988). There is no clear-cut management practice. Some evidence points towards grazing intensities that do not exceed one third of current year annual growth on key forage species (Holecheck *et al.*, 1994). This may, under favorable climatic conditions, actually improve ecological and perennial grass-cover in short time periods (Holecheck *et al.*, 1994). In addition, reduced light levels and competition with a herbaceous layer essentially stops growth of mesquite seedlings (Bush and Aiken, 1990). Combined management practices could be the solution to land encroachment if they prove to be cost-effective (e.g. Integrated Brush Management Systems, IBMS; Scifres, *et al.*, 1983; 1988).

The Rangeland Paradox

The mesquite controversy does not stand alone, as similar management practices are affecting other community structures involving woody species such as the Chaco region of South America (D'Antonio and Solbrig, 1977; Morello, 1972) and large areas of Africa (Zimmermann, 1991). The controversies surrounding these species vary greatly, however a common

denominator is the expansion of woody species towards grasslands, with a concomitant decrease in land value towards livestock grazing. The introduction of *Prosopis* into areas far from their original habitat have also affected natural vegetation and expanded rapidly. A clear example is South Africa where *Prosopis* was introduced as an agroforestry product in the 1800's, now covering approximately 180,400 ha and is currently considered an invader under the Conservation of Natural Resources Act 43 of 1983 and under an intense biological control program (Zimmerman, 1991). However, given the characteristics outlined above, conservation and management programs in arid and semi-arid environments should place a priority on the management of mesquite populations in areas depleted through conversion and its control in areas of livestock grazing as well as in areas far from its original distribution. This would provide a compromise between livestock productivity on the one hand, and conservation of species diversity and maintenance of ecosystem structure on the other.

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