

A semiarid fruit agroecosystem as a conservation-friendly option for small mammals in an anthropized landscape in Mexico

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Abstract. Many studies have addressed the potential of low-input agroecosystems for biological conservation. However, most have been carried out on annual agroecosystems in temperate, developed countries. As agricultural surface will increase and natural protected areas alone will not warrant the conservation of biodiversity, it is crucial to include different types of agroecosystems in research and conservation efforts. In Mexico, perennial, low-input, fruit-oriented nopal orchards (*Opuntia* spp.), one of the few crops suitable for semiarid areas, are the 10th out of 61 most important fruit crops grown in the country. We assessed their value for conservation in an anthropized landscape by comparing their rodent assemblages with those in adjacent habitats and determined the influence of the latter on the rodent communities inside them. We live-trapped rodents in 12 orchards and adjacent natural xeric shrubland, grassland, and cropland. We captured 19 different species, of which 17 used the orchards. Four are Mexican endemics. Orchards have higher α diversity, species richness, and abundance than cropland and grassland and are not different from shrubland. The dominant rodent species are the same in orchards and shrubland, and where these two meet they integrate into one habitat. Within-habitat quality is a critical driver of the composition and diversity of rodent communities in the orchards studied, and the neighboring habitats do not modify them substantially. Increasing within-patch heterogeneity beyond a certain level is at the expense of habitat integrity and produces small-scale fragmentation reducing habitat quality. At a landscape scale, orchards contribute importantly to regional rodent diversity compared with other land use types, and appear to increase habitat connectivity between patches of shrubland. Orchards' higher α diversity would give them higher ecological resilience and make them better suited than grassland and cropland to contribute to the conservation of local biota. Nopal orchards should be considered conservation allies and incorporated in regional conservation plans. Regrettably, their future is unwarranted as producers face low revenues and lack of governmental support. Our confirmation that orchards have an important, positive impact on biodiversity can be used as a strong argument to lobby for incentives to safeguard this environmental friendly, low-input agroecosystem.

Key words: alternate habitat; cropland; fragmentation; grassland; habitat connectivity; Llanos de Ojuelos; Mexican Plateau; nocturnal rodents; Nopal orchard; *Opuntia* spp.; prickly pear; xerophytic shrubland.

INTRODUCTION

Agricultural landscapes are one of the most extended biomes in the world, and currently occupy about 40% of the Earth's surface (Ellis et al. 2010). This agricultural expansion has been one of the main drivers of habitat fragmentation and of loss of biodiversity in a wide range of taxa (Gonthier et al. 2014). Moreover, the conversion of complex natural habitats to simplified, intensively managed monocultures and the increasing use of agrochemical for pest and weed control contribute to a reduction and loss of ecological services such as pollination (Buchmann

and Nabhan 1996, Kremen et al. 2002), pest control, and nutrient cycling (Altieri 1999, Thies and Tschardtke 1999), on which, paradoxically, crop production itself depends.

Much recent research has been aimed at uncovering the biological effects of fragmentation caused by agricultural practices and has focused primarily on the biota dependent on natural or semi-natural vegetation within the modified landscapes, and its ability to persist in them (Bennett 1990, Umetsu et al. 2008). In these studies, agroecosystems are considered collectively as a matrix that poses resistance to movements of organisms between more suitable patches.

At the same time, there is an increasing number of studies that provide strong evidence of the potential of agricultural landscapes for biodiversity conservation, especially in regions where the natural ecosystems have been modified extensively, in which some agricultural

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environments provide key habitats that sustain rich faunal assemblages (Duelli and Obrist 2003, Tschardt et al. 2005, Fahrig et al. 2011, Mellink et al. 2016). Particularly, traditional, low-intensity agroecosystems can support high species richness of different biological groups (Daily et al. 2003, Harvey et al. 2006, Perfecto and Vandermeer 2008, Riojas-López 2012, Mellink et al. 2016), or serve as stepping stones (Danielson and Anderson 1999) or corridors (Merriam and Lanoue 1990) that facilitate the movement of animals between patches. In doing so, these systems contribute importantly to biological conservation (Tschardt et al. 2005, Scherr and McNeely 2008).

At patch level, the contribution of low-intensity agroecosystems to biological conservation depends on management practices that modulate temporal and spatial within-habitat heterogeneity (Mellink 1991*a, b*, Benton et al. 2003, Riojas-López 2012) and on the presence of “keystone structures” (non-crop plants, life fencerows, rock fences; Merriam and Lanoue 1990, Tews et al. 2004, Harvey et al. 2006, Mellink et al. 2017). Although often overlooked, there is a growing body of evidence that suggests that in addition to patch-level attributes, landscape characteristics may be a significant driver of biodiversity in agricultural plots (Harvey et al. 2006, Haslem and Bennett 2008, Fahrig et al. 2011, 2015) and that species richness cannot be explained by within-patch habitat quality alone, but that external factors such boundary characteristics (Wiens et al. 1993), neighborhood (Thies and Tschardt 1999, Duelli and Obrist 2003, Bennett et al. 2006, Haslem and Bennett 2008), and matrix quality (Burel et al. 1998) also drive within-patch community composition.

The particular characteristics of neighboring habitats can affect the biological structure in individual habitat patches, but are reflected differently by different groups depending, in part, of their mobility. In a shade coffee plantation, adjacent forested areas have a positive effect on the diversity of small mammals, as some forest species are capable to move into these plantations (Caudill et al. 2014). Other studies have shown that intra-patch diversity of sessile species, like plants, depends largely on local habitat features but that bee species richness is affected by the quality of the surrounding habitat (Kremen et al. 2002, Dauber et al. 2003).

In some human-modified landscapes, low-intensity agroecosystems (i.e., agroecosystems that receive little nutrient and energy external inputs and are little mechanized), along with remnants of natural or semi-natural habitats, are “patches” embedded in more intensive agricultural land use types such as high-intensity croplands, pastures, and rangelands (Bennett et al. 2006, Fahrig et al. 2011). In these heterogeneous landscapes, biodiversity within farmland patches tends to be higher than in more uniform areas because of their continuous recolonization from complex, species-rich, nearby, semi-natural habitats (Duelli and Obrist 2003, Tschardt et al. 2008) and because of the presence of countryside elements

(trees, pasturelands; Harvey et al. 2006, Haslem and Bennett 2008).

However, much of the research has been directed to explain the effect of local features like hedgerows, grassy strips, shade provision, and vegetation structure (Merriam and Lanoue 1990, Riojas-López 2006, Perfecto and Vandermeer 2008, Vickery et al. 2009), but only a few have considered the effect of surrounding habitats on the population composition and dynamics of assemblages of wild species within complex agricultural landscapes (Dauber et al. 2003, Duelli and Obrist 2003, Thies et al. 2003, Caudill et al. 2014) or the effect of landscape composition and configuration on them (Bennett et al. 2006, Harvey et al. 2006, Tschardt et al. 2008, Fahrig et al. 2011, 2015).

Although the number of publications assessing the importance of agroecosystems for wildlife conservation has increased notoriously in the last decades, most studies are carried out in temperate, developed countries and focus on annual agroecosystems (Duelli and Obrist 2003, Batáry et al. 2011, Gonthier et al. 2014, Tuck et al. 2014), with tropical regions (Daily et al. 2003, Harvey et al. 2006, Schroth and Harvey 2007), mostly coffee agroecosystems (Perfecto and Vandermeer 2008, Caudill et al. 2014), having a modest second place. Other agricultural lands, like most low-intensity agroecosystems in arid and semiarid regions have been neglected from research. In arid and semiarid regions, traditional low-input agroenvironments, both oasis-based and rain-fed, support rich bird (Nabhan et al. 1982, Mellink 1991*a*, Rey 2011, Mellink et al. 2016, 2017) and rodent communities (Mellink 1985, 1991*b*, Riojas-López and Mellink 2005, Riojas-López 2006, 2012).

Given the great surface that agricultural landscapes cover throughout the world, the fact that this surface is predicted to increase even more (Tilman et al. 2002), and that natural protected areas alone will not warrant the conservation of biodiversity and ecosystem services (Millennium Ecosystem Assessment 2005), it is crucial to include different types of agroecosystems into agroecological research efforts (Bennett et al. 2006, Scherr and McNeely 2008, Tuck et al. 2014). This would help greatly in developing a more comprehensive framework to understand the drivers, both internal and external, that affect the within-cropland composition and population dynamics of different species and communities, and precise how local agricultural practices may help to mitigate the global loss of biodiversity.

Areas occupied by agriculture continue to expand rapidly at the expense of native habitats in Mexico. Between 1973 and 2000 the surface devoted to agriculture increased 20%, causing the loss of 17% of the 1973 cover of natural grasslands and 8% of that of shrublands (Velázquez et al. 2002). As there are no signs of a reversal in this trend, knowledge on how to design agroecosystems to aid in biological conservation is of paramount importance.

The semiarid portion of the Mexican Plateau (*sensu* Morrone 2005), where our study was carried out, is a

human-crafted landscape where farming and ranching have caused severe changes since ~400 yr ago (Riojas-López and Mellink 2005); the changes accentuating during the past 60 yr (CONABIO 1998). As a consequence, the original vegetation comprised of arboreal nopaleras (communities dominated by arboreal *Opuntia* spp., especially *O. streptacantha* Lem., *O. lasiacantha* Pfeiff., *O. chavena* Griffiths, and *O. leucotricha* D.C.), natural grasslands and shrubby oak communities have become restricted to small patches distributed in a complex landscape mosaic of annual rain-fed agricultural plots, overgrazed grasslands, secondary xeric shrublands, and perennial fruit-oriented nopal (*Opuntia* spp.) orchards (Riojas-López et al. 2011).

Nopal (“prickly pear cactus” in English; “figuier de barbarie” in French) is one of the few crops that can be cultivated in semiarid areas that are poorly suitable for rain-fed production of most fruits and vegetables and, as a result, is grown in several parts of the world, both for its fruit and for fodder (Russell and Felker 1987). In Mexico, low-input fruit-oriented nopal orchards currently cover >55,000 ha, and are the 10th most important fruit crop of 61 grown on the country, by surface planted, and the third most important of the ≥22 fruit crops native to the Americas, as well as the 14th most economically important fruit crop (data *available online*).⁴ This crop has spread from Mexico to the Mediterranean, northern Africa, Middle East, South Africa, South America, and North America where, in some areas, it covers large surfaces (Inglese et al. 2002).

Fruit-oriented nopal orchards are low-intensity, perennial agroecosystems, in which ≥30 native morphospecies derived from at least three distinct native lineages (*Opuntia ficus-indica* (L.) Mill., *O. albicarpa* Scheinvar and *O. megacantha* Salm-Dyck) are grown. Mature fruit-oriented nopal orchards are structurally diverse habitats as a result of the combination of a well-developed shrub-like nopal layer, an herbaceous stratum underneath the nopales and in the alleys between the nopal rows, and, often, isolated trees, either in the crop itself or at its edges. This agricultural habitat supports a complex suite of native rodents that includes from species typical of open grasslands to species typical of dense xeric shrublands (Riojas-López and Mellink 2005, Riojas-López 2006, 2012). At least 12 species of rodents that use the orchards, including two species that are endemic to Mexico, seem to depend strongly on them (Riojas-López 2012). Up to now most of our research effort in this agroecosystem has been directed at understanding within-orchard rodent community dynamics regardless of the surrounding landscape and other agricultural uses.

Small mammal species have long been recognized as indicators of ecological changes and ecosystem integrity. Shifts in abundance and species richness of their assemblages across landscape are useful to understand

environmental changes in both paleontological and neontological time scales (Rowe and Terry 2014). Particularly, rodents are very sensitive to change in both climate and vegetation structure and composition (Rosenzweig and Winakur 1969, Brown and Heske 1990, Riojas-López et al. 2011). Studying rodent communities in agricultural context will widen the scope of our understanding of the ecology of agroecosystems especially because most studies have addressed how agricultural practices affect bird and insect communities (as a search in the Web of Science demonstrates), but have neglected other groups, like small mammals (Thies et al. 2003, Sullivan and Sullivan 2006, Fischer et al. 2011, Caudill et al. 2014), except for pest control purposes.

The study we present here is part of an ongoing effort to understand the ecological characteristics of fruit-oriented nopal orchards in a mosaic of different land uses in the southern portion of the Mexican Plateau and to document their value for the conservation of regional wildlife, compared with other regional land uses, and was aimed at answering three questions: (1) Does adjacent habitat type influence the composition and diversity of native rodent assemblages in nopal orchards? (2) What is the contribution of nopal orchards to harbor rodent species compared with other land uses? (3) How does patch level habitat heterogeneity affect rodent communities?

METHODS

Study area and sites

This work was carried out in an area of approximately of 1,000 km² within the subprovince Los Llanos de Ojuelos in the southern portion of the Mexican Plateau (Fig. 1). Ranging from 1,800 to 2,300 m above sea level, the landscape of this region is a complex mosaic composed largely of agricultural land that includes rain-fed agriculture, perennial nopal orchards, as well as overgrazed grasslands and different classes of primary and secondary xeric shrublands, most of which are used heavily for cattle ranching (Riojas-López and Mellink 2005, Riojas-López et al. 2011).

The climate is semiarid with ~600 mm of rainfall (1969–2008 average at the Ojuelos de Jalisco weather station = 639 mm), which falls almost all during the summer. Mean annual temperature is 15°C, and pan evaporation exceeds precipitation in all months. The average monthly temperature and rainfall define three distinct climatic seasons (Mellink et al. 2016): dry-warm (from March to May), rainy (June–September), and dry-cold (November–February).

Twelve study sites, all under similar edaphic and climatic conditions, were selected based on our previous knowledge of the region, complemented by field reconnaissance specific for this project (Fig. 1). Final selection of sites depended on them being placed throughout the region as well as on logistic aspects (accessibility,

⁴ <https://www.gob.mx/siap/>

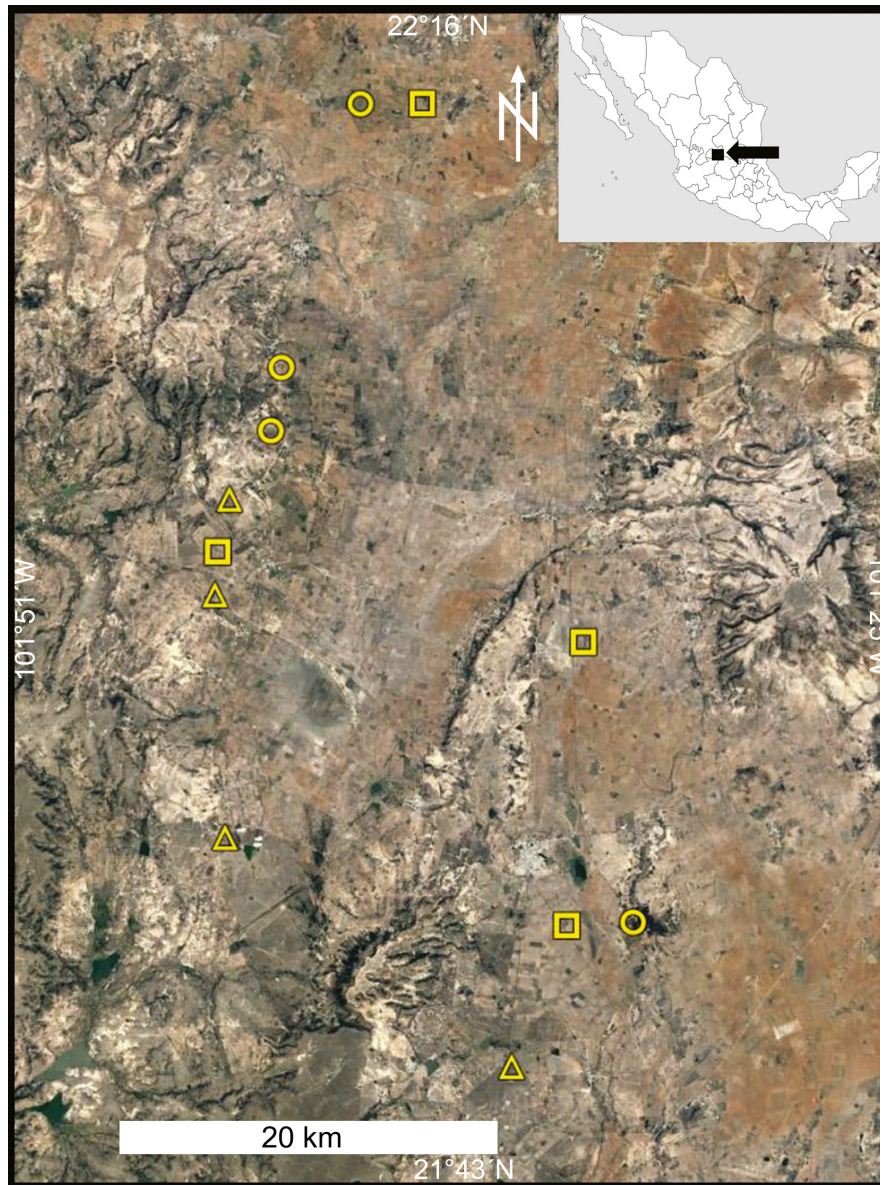


FIG. 1. Study area and study sites in Mexico. Squares indicate orchard–cropland pairs; triangles, orchard–grassland pairs; and circles, orchard–shrubland pairs. (Image source: Google Earth, ©2014 DigitalGlobe).

authorization). Each study site included two study habitats: a mature nopal orchard (≥ 4 yr of establishment) and its adjacent habitat, xeric shrubland, grassland (overgrazed), or annual rain-fed cropland. We had four sites in each combination. The adjacent habitat could surround the entire orchard, or part of it, but was never less than an entire side of the orchard. Habitat patches (orchard, adjacent) were ≥ 4 ha, and study plots were >2 km from each other.

Nopal orchards.—Most nopal orchards (hereafter orchards) in the region are managed very little, only through occasional pruning and bi-yearly applications

of manure. Most are rain fed, but some in the northern part of the area are drip irrigated for the first three years after planting, to promote establishment. Visitation by humans to the orchards is restricted largely to the cropping season, which lasts 4–6 weeks in each orchard (specific dates vary as a function of the varieties planted), but domestic animals (goats, sheep, cattle, horses) may be given access to feed on the herbage that develops after the rains, or, in years of drought, on nopal pads whose spines are previously burned by torches.

During our study, nopal plants provided 5–40% ground cover (mean = 15%, based on four 20-m Can-field lines, with a 5-cm criterion for tallying/no tallying).

Percent nopal cover did not vary depending on whether the orchard was adjacent to a shrubland, grassland, or cropland, nor between sampling periods (dry-warm, rainy, dry-cold). Overall, plant cover, composed mostly of herbs and grasses, was lower during the dry-warm (April, $37\% \pm 16\%$ [mean \pm standard deviation]) and rainy (July–August, $45\% \pm 14\%$) seasons, after which it developed to a high during the dry-cold season (late October–November; $62\% \pm 20\%$). The orchards placed in the three matrix types did not differ in their percent of total plant cover.

Xeric shrubland.—Xeric shrublands (hereafter shrubland) in the region are composed of different shrubs, mostly of Mimosaceae (*Vachellia* spp., *Mimosa* spp.), as well as several wild species of nopal (*Opuntia* spp.) and grasses (*Aristida* spp. *Bouteloua* spp., *Muhlenbergia* spp., and others), which are kept very short by heavy grazing. At some of the sites, some arboreal cover was provided by yucca trees (*Yucca decipiens* Trel.) and pirul (Peruvian Pepper, *Schinus molle* L.). Ground cover by vegetation at our study sites varied between 23% and 59%, but there was no seasonal pattern, perhaps because of grazing by livestock arrested plant growth after the raining season. Total plant cover was similar to that of the grassland sites, and much higher than that of the cropland sites.

Overgrazed grassland.—Grasslands were one of the dominant vegetation types at the arrival of European colonizers, but have since been altered heavily by grazing by domestic livestock (Riojas-López and Mellink 2005). Currently, grasses in them are kept very short, almost to the ground, by intensive grazing, mostly by sheep. Grasslands are currently composed of some grazing-resistant species (*Bouteloua* spp. and others), which covered 18–43% of the ground in our plots. They also had perennial herbs (*Eryngium comosum* F. Delaroché, *Evolvulus* spp., *Dichondra argentea* Humb. & Bonpl. ex Willd and *Astragalus* spp.), scattered shrubs (*Isocoma veneta* (Kunth) Greene, *Jatropha dioica* Sessé ex Cerv., *Vachellia schaffneri* (S. Watson) Seigler & Ebinger), and, sometimes, yucca trees. Plant cover was similar to that of the shrubland sites, and much higher than of the cropland sites.

Annual cropland.—In our study region, the growing of annual crops (hereafter cropland) are mostly restricted to corn and beans, although some small cereals, especially barley and wheat, are also grown. Almost all is rain fed and, as a result, plant cover on cropland sites varied from 0% to 30%, depending on summer rains, and the phenology of the crops and ruderal herbs associated, and on whether some winter rain had fallen early in the year. Overall, plant cover was much lower than that of shrubland and grassland sites.

Rodent sampling

Within each habitat patch (orchard, adjacent) of each study site we placed 45 Sherman live-traps baited with

oatmeal and vanilla extract in a 15×3 grid. Grids were placed >60 m from the patch border, to prevent the influence of a border effect. Trap lines were parallel and 20 m apart, while within lines, traps were spaced 10 m apart. The two plots in each pair were surveyed simultaneously during two consecutive nights.

All individuals captured were identified in situ to species, following Hall (1981) and our own notes based on previous museum work. All individuals were marked with non-toxic permanent ink on the base of the tail, and released unharmed immediately after on the spot. Handling always took <3 min and often <1 min. Rodent sampling procedure does not contravene any procedures by the Dirección General de Vida Silvestre, the Mexican authority that regulates research in natural communities, nor those of the Universidad de Guadalajara.

Our study involved sampling of all sites once in each one of the climatic seasons in 2011: 23 March–12 April (dry-warm), 18 July–3 August (rainy), and 21 October–6 November (dry-cold). The order in which we sampled the sites followed logistic considerations, was different in the three sampling periods and in none followed a geographical trend.

We compared rodent assemblages between the three orchards groups (those adjacent to each of the habitat types), and between orchards and the other habitat types in terms of abundance, species richness (hereafter richness), and alpha and gamma taxonomic diversity. Rodent abundance was estimated as the number of different individuals captured of each species per plot and sampling period.

Habitat richness was considered as the total number of different species recorded per plot and sampling period. Habitat alpha diversity (within-habitat taxonomic diversity, hereafter α diversity) was calculated as the mean of the exponential function of the Shannon entropy index ($\exp^{H'}$; Jost 2007) for each plot and each sampling period, averaging the values for each habitat type ($n = 12$ for each adjacent habitat type, $n = 36$ for orchards). Habitat gamma diversity (accumulated taxonomic diversity, hereafter γ diversity) was calculated using the pooled data of all periods and plots per habitat type. Beta diversity (hereafter β diversity), calculate as γ diversity/ α diversity, allowed us to explore species turnover within the habitats studied. Averaging all individual plot/season values and calculating the diversity value of all pooled data we calculated α , γ , and β landscape-diversity values in the same way.

To calculate the similarity between orchards within orchard groups (as defined by their adjacent habitat: cropland, grassland, shrubland) and how similar the orchards were to their adjacent habitat, also within each adjacent habitat, we used a percentage similarity coefficient.

Intra-patch heterogeneity

In arid and semiarid environments, habitat structural heterogeneity (hereafter, heterogeneity) has an

important effect on the composition of rodent communities (Rosenzweig and Winakur 1969, Brown and Zeng 1989, Riojas-López 2012). We used two intra-patch habitat heterogeneity proxies: the vertical structure of the vegetation and a habitat heterogeneity value. We approximated habitat heterogeneity through the exponential function of the Shannon entropy index, based on the cover of each growing form obtained through four 20-m modified Canfield lines, with a 5-cm criterion for tallying/no tallying (Herrick et al. 2005), and the proportion of ground not covered by vegetation; i.e., covered with litter or of bare soil. Growth forms were herbs, low (0–20 cm), medium (21–40 cm), and tall (>40 cm); shrubs, low (20–60 cm), medium (61–120 cm), and tall (>120 cm); and open spaces (bare soil + litter patches).

Data analysis

To test whether the adjacent habitat type and season (categorical variables) had an effect on orchard (1) rodent total abundance, (2) species richness, (3) α , γ , and β diversity, and (4) heterogeneity values, we used two-way analysis of variance (ANOVAs) for normally distributed data. Abundance and species richness were square-root-transformed to meet ANOVA assumptions. Whenever significant differences were detected we used Tukey's test to compare the means. We followed the same procedure to compare rodent community variables in orchards vs. their adjacent habitat. In this comparison, when data were not normally distributed, we used Kruskal-Wallis tests, followed by pairwise comparisons when significant differences were found. Differences in similarity values were explored through ANOVAs of arcsine-transformed values (percentage similarity coefficient \times 100), as follows: (1) between the orchards as a function of the adjacent habitat, by season; (2) between the adjacent habitat plots belonging to same habitat type, by season; and (3) between each orchard and its adjacent habitat, by season. All results were considered significant at $\alpha \leq 0.05$, unless otherwise stated in *Results*.

To explore whether rodent assemblages were influenced by habitat type and orchard group (as defined by their adjacent habitat) we employed a principal component analysis (PCA) based on rodent abundance at all sites and seasons. We excluded from this analysis species of which only one individual was trapped in the whole study. We used Jackson's broken-stick test (Jackson 1993) to determine whether the percentage variation explained by the axis was higher than that given by random expectation. The arrangement of different habitats along the axes that were non-randomly organized (only axis 1) was compared through an analysis of variance and further explored with a Fisher post-hoc test. We explored the effect of habitat complexity on rodents by plotting rodents α diversity and abundance (square-root-transformed) vs. habitat heterogeneity, and rodent richness vs. habitat heterogeneity, and searched for the best relation between them through general regression

models. In all cases, we removed the outliers. Finally, we used Kruskal-Wallis tests to test for differences in abundance of some selected rodent species as a way to detect if they preferred or avoided any of the studied habitats.

Scientific names follow the Interagency Taxonomic Information System data base (ITIS; *available online*).⁵

RESULTS

Rodents in orchards and adjacent habitats

Throughout the study, we captured 962 individuals of 19 different species of nocturnal rodents, out of 25 potential species known for the region. The orchards are used by 17 different species, four of them endemic to Mexico, of which one is microendemic to the Mexican Plateau. Cropland patches are used by six species (including the microendemic and one endemic), grasslands by five (including two of the endemics), and shrublands by 13 (including the three endemics; Fig. 2).

Species richness, abundance, and α , γ , and β diversity values of rodent assemblages in orchards are not significantly different between orchards bordering shrubland, grassland, or cropland (Table 1). Orchards adjacent to grassland and cropland have rodent assemblages that are richer, have more individuals, and have higher values of α diversity than their adjacent habitats. In contrast, orchards adjacent to shrubland are not statistically different from it in any of these parameters (Table 1). Overall γ and β diversity values in orchards are 7.6 and 2.54, respectively.

Rodent assemblages in shrubland have significantly higher abundance, richness, and α diversity than either cropland or grassland, which are not different from one another. Overall landscape γ and β diversity values are 9.08 and 2.74, respectively (Table 1). Orchards contribute 84% to the landscape γ diversity; cropland, 38%; grassland, 35%; and shrubland, 85%.

Similarity between orchard groups is significantly different depending on the adjacent habitat ($F_{2,49} = 3.34$; $P = 0.04$; Fig. 3). Rodent assemblages in orchards adjacent to grassland are more similar to each other than those in orchards neighboring shrubland or cropland. Rodent assemblages in orchards are significantly more similar to each other than the assemblages within each of the three adjacent habitat types (Fig. 3). Likewise, orchards and their adjacent shrubland are significantly more similar than orchard–grassland and orchard–cropland pairs ($F_{2,31} = 12.6$, $P < 0.01$). Season does not cause significant differences in any of the variables, neither in orchards nor in adjacent habitats.

Individual species in orchards and adjacent habitats

Liomys irroratus (Gray, 1868), *Peromyscus maniculatus* (Wagner, 1845), and *Reithrodontomys fulvescens* J.A.

⁵ https://www.itis.gov/about_itis.html

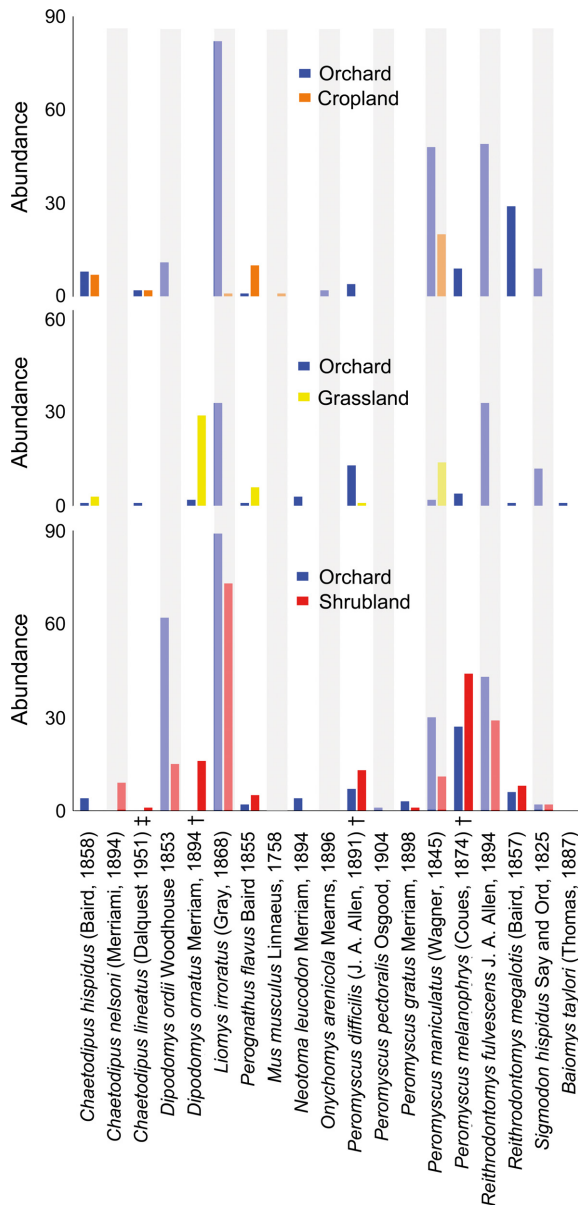


FIG. 2. Total rodent abundance in pairs of orchard-adjacent habitat. Abundance is the sum of total different individuals trapped. Symbols indicate microendemic (‡) and endemic (†) species.

Allen, 1894 are the three most abundant species throughout the study, accounting for 57% of the total rodent abundance. Three of the species, *L. irroratus*, *Peromyscus melanophrys* (Coues, 1874), and *R. fulvescens* are significantly more abundant in orchards and shrubland than in grassland and in cropland (Kruskal-Wallis $H = 29.6, 16.7, \text{ and } 23.7$, respectively; $P < 0.01$ in all cases). *Sigmodon hispidus* Say and Ord, 1825 is more abundant in orchards than in any other habitat type ($H = 9.1, P = 0.02$); *Peromyscus difficilis* (J.A. Allen,

TABLE 1. Comparisons of rodent species richness, abundance, and taxonomic diversity between groups of nopal orchards adjacent to different habitats, and between orchards and these adjacent habitats, in the Llanos de Ojuelos, Mexico.

	Between orchard groups (F, P)		Orchard-adjacent habitat pairs (F, P)			
	Orchard	Crop	Orchard – Grass	Orchard – Shrub	Orchard – Shrub	(F, P)
Richness	4.4 ± 0.6^a	1.4 ± 0.2^b	3.7 ± 0.2^a	1.6 ± 0.7^b	4.8 ± 0.7	(0.03, 0.92)
Abundance	21.1 ± 5^a	3.4 ± 0.7^b	8.9 ± 1^a	4.4 ± 1.3^b	23.3 ± 4.3	(0.57, 0.45)
α -diversity	3.7 ± 0.6^a	1 ± 0.2^b	3.2 ± 0.2^a	1.3 ± 0.3^b	3.7 ± 0.4	(0.45, 0.5)
γ -diversity	6.6^a	3.5^b	6.1^a	3.2^b	7.7	(0.10, 0.76)
β -diversity	2	2.7	1.9	2	2	(0.16, 0.69)

Notes: All values are mean \pm SE. Taxonomic diversity values are \exp^H .

Orchard groups are those formed by the orchards adjacent to shrubland, to grassland, and to cropland.

Values of orchard-adjacent habitat comparisons with different letter are significantly different ($\alpha \leq 0.05$). Lack of letter indicates that the means are not significantly different.

γ -diversity value of shrubland is significantly higher than that of cropland and grassland, which are not significantly different ($F_{3,20} = 0.79, P < 0.01$).

Degrees of freedom for F in orchard – adjacent comparisons were 1 and 20, except in γ - and β -diversity, when they were 1 and 6.

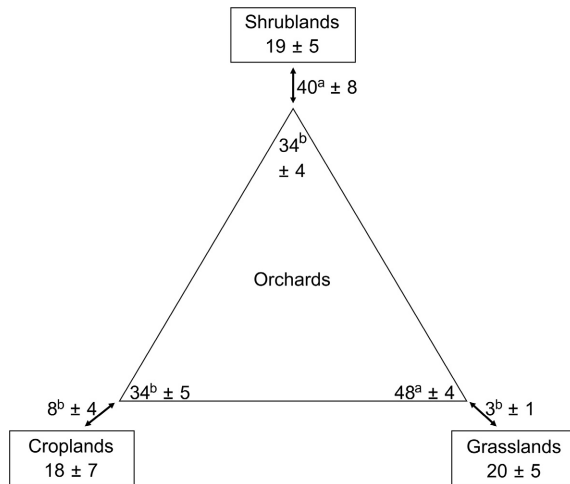


FIG. 3. Similarity values (%; mean \pm SE) within and between habitat groups. Values in each angle of the triangle represent similarity between the orchards associated with each of the adjacent habitat types indicated opposite. Values inside the rectangles are similarity values between study plots within each type of habitat indicated. Values next to the arrows are similarity values between each orchard and its corresponding adjacent plot, within the habitat indicated. Values with the same letter within each group (triangle, rectangles and arrows) are not statistically different ($P \leq 0.01$ in all cases).

1891) ($H = 9.3$, $P = 0.02$) and *Dipodomys ordii* Woodhouse, 1853 ($H = 9.46$, $P = 0.02$) are more abundant in shrubland. The species that prefer orchards and or shrubland avoid cropland and grassland (Fig. 2). *Dipodomys ornatus* Merriam, 1894 is more abundant in grassland and shrubland ($H = 22.16$, $P < 0.01$), while *Onychomys arenicola* Mearns, 1896 and *Neotoma leucodon* Merriam, 1894 were captured only in orchards (Fig. 2).

Habitat heterogeneity and its relation to rodent communities

Heterogeneity does not differ significantly between the orchards as a function of the type of adjacent habitat ($F_{2,31} = 0.09$, $P = 0.90$; Fig. 4). Orchards are as heterogeneous as the shrubland adjacent to them, and significantly more than their adjacent grassland and cropland ($F_{2,66} = 30.05$, $P < 0.01$; Fig. 4). During the dry-warm season, orchards are significantly less heterogeneous than in the dry-cold and rainy seasons (Table 2, $F_{2,31} = 6.34$, $P < 0.01$), whereas none of the adjacent habitats exhibit a seasonal effect on habitat heterogeneity.

When explored through a PCA, only axis 1 explains enough variance (24% of total variance) to be considered different from random expectation, by Jackson's broken-stick test. The study sites follow a general gradient of habitat complexity along the axis, from grassland and cropland on the left side to shrubland and orchards in the middle and right side, but the arrangement is not perfect as there is some interspersed among the

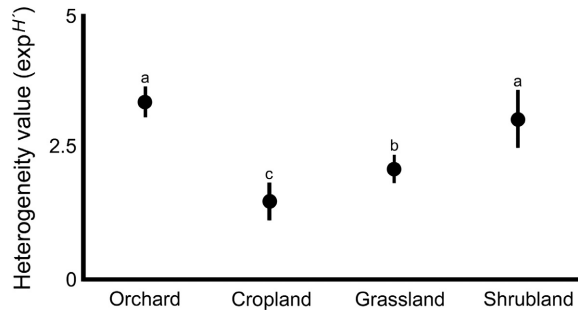


FIG. 4. Habitat heterogeneity values (exponential function of Shannon entropy index) of nopal orchards and their adjacent habitats. Heterogeneity values were calculated with the cover of the different plant growth forms and plant height categories (see *Methods*) and the proportion of open spaces (bare soil and soil covered by litter; mean \pm SE). Data points with the same letter are not significantly different ($P \leq 0.01$).

different habitat types (arrangement sequence was: G, S, C, C, G, G, S, C, G, N, N, C, N, N, N, N, N, N, S, N, S, N, N; where G is grassland, S is shrubland, C is cropland, and N is nopal orchard). When the scores of the different habitats along axis 1 are compared, orchards are significantly different ($P \leq 0.05$) from grassland and cropland but not from shrubland; shrubland is different ($P = 0.07$) from grassland but not from cropland; and there are no differences between cropland and grassland. Polynomial regressions offer the best fit of rodent richness ($R^2 = 0.27$, $P < 0.01$), abundance ($R^2 = 0.18$, $P < 0.01$), and α diversity ($R^2 = 0.26$, $P < 0.01$) on habitat heterogeneity (Fig. 5). In the three cases, richness and α diversity reach their maxima at mid-levels of habitat heterogeneity rodent abundance, after which they decrease.

DISCUSSION

The study we report here is one of the few that addresses the potential of low-input agroecosystems for biological conservation in a semiarid region, focuses on rodents, and incorporates the effect of surrounding habitats. Nopal orchards in our study harbor 17 species of rodents, all of which are typical of xeric habitats in the region (Riojas-López 2006, 2012). Individual orchards have as little as one species, or as many as nine.

Our findings exhibit that within-habitat quality is a critical driver of composition and diversity of rodent communities in nopal orchards and that the neighboring habitats here studied do not modify substantially the orchards' rodent assemblages. More heterogeneous habitats tend to have more species than less heterogeneous habitats (Rosenzweig and Winakur 1969, Price and Brown 1983, Mellink 1991b, Sullivan and Sullivan 2006). In our case, both orchards and shrubland have larger and more complex rodent communities than the structurally much simpler cropland and grassland. Even within orchards, habitat heterogeneity is an overall

TABLE 2. Seasonal variation in habitat heterogeneity of four common habitats in the Llanos de Ojuelos.

Habitat type	Season			ANOVA
	Dry-warm	Rainy	Dry-cold	
Cropland	1.25 + 0.18	1.24 + 0.14	1.95 + 0.28	$F_{2,9} = 3.6, P = 0.07$
Grassland	2.09 + 0.22	1.93 + 0.11	2.27 + 0.20	$F_{2,9} = 0.80, P = 0.47$
Shrubland	2.93 + 0.64	2.53 + 0.28	2.45 + 0.36	$F_{2,9} = 0.06, P = 0.93$
Orchard	2.78 + 0.19 b	3.56 + 0.19 a	3.74 + 0.19 a	$F_{2,33} = 6.71, P < 0.01$

Notes: Values are mean ± SE of \exp^{H^I} .

Values in the same row with the same letters are not significantly different ($\alpha \leq 0.05$).

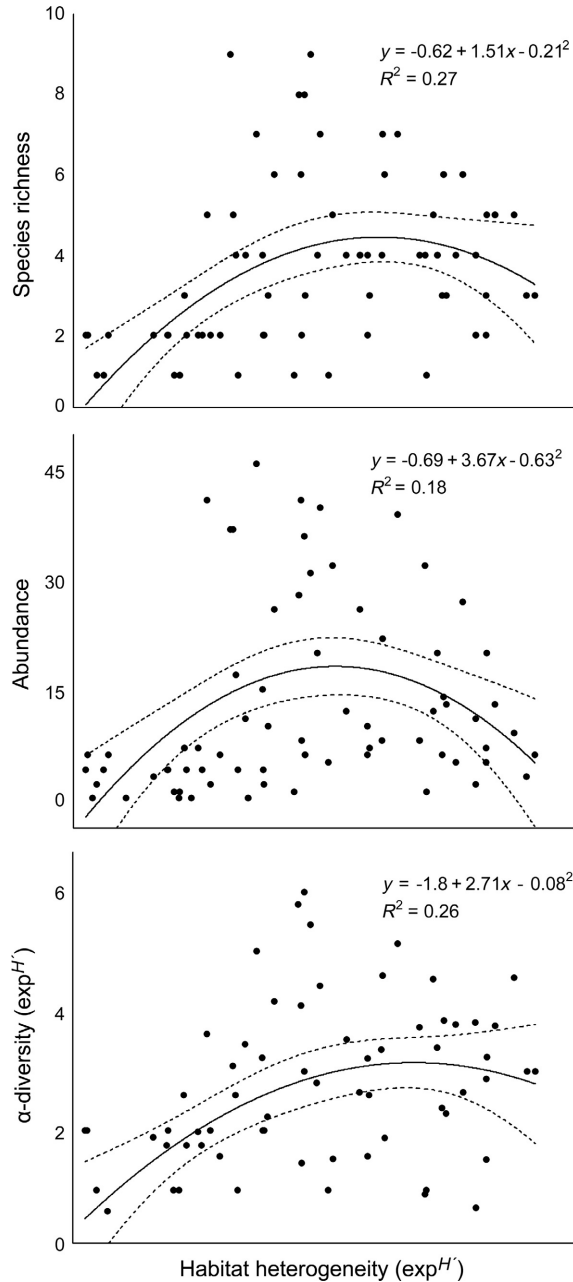


FIG. 5. Effect of within-habitat heterogeneity on rodent species richness, abundance, and α diversity taxonomic values.

driver of rodent communities, as is demonstrated by their arrangement through a PCA. It follows a gradient from lower to higher habitat complexity regardless of the type of habitat the orchards are adjacent to; the placing of the orchards on the axis is significantly related to their values of habitat heterogeneity (regression analysis, Spearman's coefficient = 0.45, $P < 0.05$). There are no significant differences in habitat heterogeneity between the orchard groups, but that does not mean orchards were the same; it is just that orchards are more similar or more different from each other regardless of the type of adjacent habitat.

The orchards exhibit seasonal variations in habitat structure, while the other habitats studied do not. Restriction of grazing by domestic animals in orchards allows the herbaceous vegetation to develop according to the rainfall amount and pattern, whereas in grassland and shrubland, unrestricted grazing prevents development of a good herbaceous community. The timing of our surveys did not allow us to record the presence of a full-grown herbaceous cover in cropland.

Compositional heterogeneity at the landscape level has a positive effect on biodiversity (Harvey et al. 2006, Haslem and Bennett 2008, Fischer et al. 2011). General management practices of nopal orchards in the region include applying manure and weeding, but when and what kind of manure to apply, when and how to weed, and what other practices to apply depend on individual decisions by the owners. This confers a great compositional heterogeneity and is reflected in the orchards having 2.54 different subsets (orchard β diversity) of the total orchard rodent species pool, and them being only slightly similar to each other ($36\% \pm 2.5\%$; mean ± SE).

The set of numerically dominant rodent species in all orchards is the same as that in shrubland, and rodent assemblages are five times more similar to each other in orchard–shrubland pairs than the assemblages in orchard–grassland and in orchard–cropland pairs. Where orchard and shrubland meet, they are perceived by the rodents as a single habitat. These orchard–shrubland pairs have greater rodent similarity even than orchards with other orchards.

Habitat structure and heterogeneity (sensu Rosenzweig and Winakur 1969, Brown and Zeng 1989, Riojas-López 2012) lie behind the similarities and differences between rodent assemblages in nopal orchards and their adjacent

habitats. For example, both *L. irroratus* and *P. melanophrys* prefer habitats with medium cover at ground level but good cover by shrubs; while of *R. fulvescens* prefers sites with extensive herbaceous cover at ground level and *D. ordii*, shrubland with a large proportion of open patches. These four species are abundant in both orchards and shrubland, but not in cropland and grassland.

Orchards and shrubland differ neither in habitat heterogeneity, nor in their rodent community attributes, although some differences exist in individual species. *Dipodomys ornatus* has its highest numbers in grassland and was captured in shrubland as well, but not in the orchards adjacent to it. We do not have a good explanation for this, but it merits further investigation as the species is included in Mexico's species at risk list (SEMARNAT 2010). Another species, *N. leucodon*, typically uses shrublands with clumps of wild nopalles (*Opuntia* spp.; Rangel and Mellink 1993 [as *Neotoma albigula* (Hartley, 1894)]) as well as nopal orchards (Mellink and Riojas-López 2002, Riojas-López 2012). Unexpectedly, in this study we captured it in orchards only and not in shrubland. This suggests the existence of subtle habitat differences finer than those addressed by us, and about which we have no explanation at this time.

Past studies have documented that neighborhood habitats affect diversity and community composition in farmland patches (Burel et al. 1998, Thies and Tscharnkte 1999, Kremen et al. 2002, Dauber et al. 2003, Caudill et al. 2014). To the contrary, in our study, rodent community attributes in nopal orchards are not affected strongly by the type of neighboring habitats, evidencing that some forms of agriculture develop complex internal biotic relationships and interactions that are above the effect of adjacent habitats, and that intra-patch heterogeneity is a stronger ecological driver than the features of surrounding habitats. Nonetheless, this does not mean the orchards do not exhibit any neighboring habitat effect at all. There is one slight difference between orchards groups: orchards adjacent to grassland are 41% more similar to each other than those neighboring cropland or shrubland. This is explained mostly by the absence of *D. ordii* and *Reithrodontomys megalotis* (Baird, 1857) from the orchards adjacent to grassland. Such absence is likely not driven by habitat features within the orchard, as habitat heterogeneity and ground cover by plants do not differ between orchard groups. It might rather result from the absence of the two rodent species from grassland. Despite this effect, rodent assemblages of the orchards are more alike each other than those of shrubland, grassland, and cropland are to the same-habitat patches across our study.

Many rodent species increase their exploratory behavior when faced with rapidly changing landscapes and, even in the absence of well-established corridors, can reach suitable habitats if they find adequate "stepping stones" (Kozakiewicz and Szacki 1995). Corridors or stepping stones can arise with the development of

certain ephemeral habitats and facilitate rodent dispersion across "hostile matrices" (Merriam and Lanoue 1990, Danielson and Anderson 1999, Fischer et al. 2011). Our study did not have the temporal resolution needed to detect such ephemeral corridors, but both cropland and shrubland (but not grassland) during the growing season of some years develop dense herbage cover, becoming ephemeral occupancy habitat, corridors, or stepping stones, and promoting regional population increases of some rodent species (Mellink 1991b), allowing their dispersion between habitats that are permanently suitable and promoting colonization where a species might have disappeared. Thus, orchard rodents, despite being surrounded by low-quality habitats, in many cases do not find these surroundings permanently hostile, but interact with them in dynamic and complex ways. In the end, the orchards are not isolated, but connected by patches with different cover types throughout the landscape, either permanently or ephemerally.

The conversion of wild habitats to agriculture usually leads to a process of biotic homogenization and a decline in species richness (McKinney and Lockwood 1999). Rather than this, nopal orchards perform a double role in the amelioration of conservation problems in our study region. On one hand, they contribute importantly to retain the regional rodent diversity compared with other types of agricultural lands uses, not only because of the proportion of the regional species pool they harbor, but also because the four rodent species endemic to Mexico in the region find habitat in them: *P. melanophrys*, *P. difficilis*, and *D. ornatus* (the three moderately restricted, sensu Tambutti et al. [2002]) and *Chaetodipus lineatus* (Dalquest, 1951) (highly restricted). The latter species is endemic to a very small area of the Mexican Plateau and its population status is considered fragile or vulnerable (Ortega and Arita 2014). On the other hand, our data suggest that orchards increase habitat connectivity between patches of shrubland, reducing the risk of reaching local extinction thresholds at least for shrubland rodent species; they do so, albeit to a lesser degree, for some grassland rodent species as well.

At a patch scale, orchards have higher α diversity than cropland and grassland, which would imply that orchards have higher ecological resilience (sensu Duelli and Obrist 2003). As a more stable system, nopal orchards are better suited than other agricultural land uses in the region to contribute to the conservation of local biota. Not only do they provide food and shelter for many different rodent species, but, in doing so, they provide also prey for other vertebrates.

The unexplained portion of the association between habitat heterogeneity and rodent species richness, abundance, and α diversity might reflect differences in productivity between the habitats studied. In general, as productivity increases, diversity increases (Brown 1981), and areas with higher productivity have also more rodent species (Brown and Lieberman 1973). Nopal orchards can be highly productive at different levels,

including herbs and shrubs and their seeds, tunas (prickly pear fruits), and invertebrates; all of which represent resources for the rodents and would influence their assemblages.

Other studies performed in agricultural habitats have found that an increase in structural habitat diversity has a positive effect on small mammals' diversity (e.g., Sullivan and Sullivan 2006). Our data reveal one unexpected pattern: after reaching a maximum, rodent species richness, abundance, and α diversity diminish with increasing habitat heterogeneity. Thus, increasing within-patch heterogeneity beyond a certain level is at the expense of habitat integrity and produces small-scale fragmentation in which patches of quality habitat (food and cover) for some species become too small. Structural habitat attributes that are perceived as heterogeneous by one species could be perceived as fragmented by another, as the habitat attributes that promote diversity become too limited to support any population. The same effect, at pertinent scales, should be expected for other groups of animals.

Although several aspects of the relationship between the local landscape's characteristics and components and biodiversity remain to be studied, we can firmly assert that nopal orchards play an important role in the conservation of biodiversity. They provide adequate habitat for the majority of the rodent species in our study area (17 species of 25), especially for shrubland-loving species. For grassland rodent species, orchards can be neutral or beneficial, but not dangerous, not even for *D. ornatus*, which in this study seems to avoid them, but which we have previously captured in high numbers in other nopal orchards in the region (Riojas-López 2006, 2012; as its synonym: *Dipodomys phillipsii* Gray, 1841). The habitat attributes that make some orchards but not others adequate for this species should be elucidated.

Regrettably, despite their important conservation role, the future of nopal orchards is not warranted as tuna producers face low revenues and lack of governmental support, contrasting with other crops, which in our area are highly unreliable and environmentally less friendly but which receive subsidies. Our confirmation that orchards have an important, positive impact on biodiversity can be used as a strong argument for the support of nopal growers to lobby for incentives to maintain the use of this environmentally friendly, low-input agroecosystem.

One final remark is in order. Despite their conservation potential, nopal orchards should not be seen as a substitute for native vegetation, and we strongly recommend preserving shrubland and improving the condition of natural grasslands in the region. Along with this, nopal orchards must be considered conservation allies and incorporated into regional conservation plans.

CONCLUSIONS

We reach the following conclusions. (1) Nopal orchards play an important role in the conservation of local

populations of native rodents. They have larger and richer rodent communities than grasslands and annual croplands in the region, sustain 85% of the regional rodent diversity, and seem to increase habitat connectivity. (2) Rodents depended largely on within-patch structural habitat attributes, and are affected little by those of adjacent habitats. (3) When adjacent to shrubland, orchards form a single habitat unit with shrubland in which the individual rodent assemblages are much more similar than in orchard–grassland, orchard–cropland, and even orchard–orchard pairs. (4) Beyond a certain point, increases in within-habitat heterogeneity affect rodent community attributes negatively because of small-scale fragmentation. (5) Our confirmation that orchards have an important, positive impact on biodiversity can be used as a strong argument to lobby for incentives to safeguard this environmentally friendly, low-input agroecosystem.

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DATA AVAILABILITY

Data available from the Institutional Repository of the University of Guadalajara (RIUdeG): <http://repositorio.cucba.udg.mx:8080/xmlui/handle/123456789/6015>.