Patterns of shrub-dwelling arthropod diversity across a desert shrubland–grassland ecotone: a test of island biogeographic theory

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This study tested the applicability of Island Biogeographic Theory to arthropod assemblages on ‘islands’ of creosotebush (*Larrea tridentata*) across a desert shrubland-grassland ecotone in central New Mexico, U.S.A. We assumed that herbivorous arthropod taxa that specialize on creosotebush view these shrubs as ‘islands’ of suitable habitat in a ‘sea’ of grassland, and used the Island Biogeographic Theory to examine the observed plant and arthropod patterns. Specifically, we addressed predictions concerning the relationship among arthropod species richness and (1) shrub ‘island’ area, (2) distance between ‘island’ and ‘continent’, and (3) ‘island’ isolation. Using a pyrethrum insecticide, we defaunated 36 shrubs within three ecotonal areas (12 shrubs per area), defined as ‘continental’ (high shrub density), ‘archipelago’ (medium shrub density, close to the ‘continent’), and ‘oceanic’ (low shrub density, far from the ‘continent’). We assessed the initial arthropod distribution and then repeated the defaunation after two weeks to assess immigration patterns. The arthropods from both samples were catalogued and related to ‘island area’ (shrub volume), ‘island’ distance from the defined ‘continent’, and ‘island’ isolation (density). We found that in the initial sample, specialist herbivore species richness was (1) positively related to shrub volume, (2) negatively related to shrub distance from the ‘continent’, but (3) not significantly related to shrub density. Following the recolonization period, we found that specialist herbivore species richness was again significantly positively related to shrub volume, but was not significantly related to shrub distance from the ‘continent’ or to shrub density. We also examined the relationship between generalist predator arthropod (spiders and mantids) populations and shrub ‘island’ characteristics as well as specialist prey abundances on the shrubs. We found that predator abundances on individual shrubs were positively related to shrub volume prior to and following defaunation, negatively related to shrub density both initially and following recolonization, and positively related to the architectural complexity of host shrubs initially. We also found that predator population sizes on shrubs were positively correlated with abundances of specialist prey species. We concluded that our model conformed fully to the species richness–island area and species richness–island distance relationships of Island Biogeographic Theory, but only in part to the species richness–island isolation relationship. We also found that species-specific dispersal ability was a critical factor with regard to the observed species distribution patterns.

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**Keywords**: Island biogeography; creosotebush; *Larrea tridentata*; Arthropoda
Introduction

Island Biogeographic Theory (MacArthur & Wilson 1963, 1967) has served as a model with which to predict insular species richness and turnover rates in relation to island size and isolation. Since its inception, the theory has been subjected to extensive experimentation using actual island systems as well as systems composed of ‘islands’ of suitable habitat. The theory’s principles have aided in the explanation of species distribution (e.g. Diamond, 1972) and recolonization patterns (e.g. Thornton et al., 1993) of various oceanic archipelagoes, as well as isolated mountaintops (Brown, 1971, 1978) and isolated patches of montane forest (Lomolino et al., 1989; Kratter 1992; Lomolino & Davis, 1997). In addition to its application to naturally occurring species distribution patterns, it has also been tested experimentally with regard to the defaunation of islands as a means to observe recolonization patterns following an extinction event (Simberloff & Wilson, 1969, 1970; Wilson & Simberloff, 1969).

Global climate change and human land use practices in arid and semi-arid ecosystems have resulted in desertification processes and ecotonal shifts; in some instances, these occurrences have resulted in the invasion of desert grasslands by woody shrubs (Schlesinger et al., 1990). Over the past century, the desert grasslands of the southwestern United States have experienced such desertification and the encroachment of mesquite (Prosopis spp.) and creosotebush (Larrea tridentata) (York and Dick-Peddie, 1969; Hennessey et al., 1983).

Creosotebush acts as the exclusive host to a number of highly specialized arthropods (Hurd & Linsley, 1975; Schultz et al., 1977). In regions where creosotebush has invaded grasslands, these specialist arthropod species also have successfully established permanent populations. While it is clear that creosotebush characteristics affect associated herbivorous arthropod distributions (Lightfoot & Whitford 1989, 1991), the patterns of arthropod assemblages across changing ecotonal boundaries (e.g. shrub invasions) are not fully understood.

This study evaluated arthropod distribution patterns across a shrubland-grassland ecotone in central New Mexico through an application of Island Biogeographic Theory. Similar to Brown & Kodric-Brown (1977), we considered individual plants, in this case creosotebushes, as ‘islands’ of suitable habitat for specialist and non-specialist arthropods. We tested theoretical predictions as to how creosotebush range expansion might affect arthropod distribution across this shrubland-grassland ecotone.

We examined three major components of the theory in the assumed equilibrium (initial) and non-equilibrium (recolonized) stages of arthropod turnover rates on the shrubs, namely the species richness–island area, species richness–island distance, and the species richness–island isolation relationships. First, we asked how species distributions across this ecotone aligned with the theoretical prediction that, at equilibrium, larger shrubs would have higher species richness than smaller shrubs, and that more distant and more isolated shrubs would have lower species richness than shrubs in high-density, extensive patches (i.e. ‘continents’). Second, we examined the degree to which the recolonization pattern (following experimental ‘extinctions’) of these ecotonal creosotebushes, in the non-equilibrium stage, concurs with the theory’s prediction that recolonization takes place at a relatively higher rate on less isolated shrubs. Furthermore, to explore the patterns of predator populations (spiders and mantids) and their prey (the specialist herbivores) on these shrub ‘islands’, we examined predator distributions and abundance patterns with respect to shrub size, distance, isolation, prey abundances and shrub architectural complexity.
Methods

Study site

The study was conducted on the Sevilleta National Wildlife Refuge (NWR), Socorro County, New Mexico, U.S.A. The Sevilleta NWR encompasses nearly 100,000 ha, and straddles the transition zone between the northern Chihuahuan Desert and the Great Plains short grass steppe. A former Spanish Land Grant and cattle ranch, the Sevilleta NWR was established in 1974, and all livestock were removed during 1974–1975. Since that time, the refuge has been managed by the U.S. Fish and Wildlife Service as a preserve for research and environmental education.

The study area was located on the ecotone between Chihuahuan Desert shrubland and a flat, grassy plain, known locally as McKenzie Flats (latitude 34°20′30″N, longitude 106°42′30″W, elevation 1600 m; Fig. 1). The shrubland was composed of a dense stand of creosotebush, with scant intervening herbaceous vegetation. The grassland was dominated by a variety of grasses, including black grama grass (Bouteloua eriopoda), blue grama grass (B. gracilis), purple three-awn (Aristida purpurea), fluff grass (Erioneuron pulchellum) and several dropseeds (Sporobolus flexuosus, S. contractus, and S. cryptandrus). Common forbs included Indian rushpea (Hoffmannseggia glauca), globemallow (Sphaeralcea fendleri), bladderpod (Lesquerella fendleri), and several species of spurge (Chamaesyce spp.). Individuals and small patches of creosotebush occurred across the grassland, with overall shrub densities declining northward with greater distances from the grass-shrub ecotone. Other scattered shrubs included four wing saltbush (Atriplex canescens) and snakeweed (Gutierrezia sarothrae). Soils were classified as Berino-Dona Ana association, consisting of fine-loamy, mixed, thermic Typic Haplargids. Mean annual precipitation was 244 mm, with a mean daily minimum temperature of −7.3°C in January and a mean daily maximum of 33.2°C in July (Sevilleta LTER meteorological data, Deep Well weather station, 1988–2000).

Field sampling

Arthropod assemblages were sampled on 36 individual creosotebushes from across this shrubland–grassland ecotone on 18–25 July 2000. Shrubs were located in three regions of the ecotone (12 per region), representing the three levels of ‘island’ isolation (Fig. 1): (1) ‘continental’ shrubs were selected within the high-density expanse of creosotebush along the ecotonal boundary; (2) ‘archipelago’ shrubs were selected within the medium-density, mixed stands of grasses and creosotebush; and (3) ‘oceanic’ shrubs were selected within the low-density, grass-dominated area of the study site. The 12 continental and archipelago shrubs were selected at three sites (four per site) within their respective regions, whereas the twelve oceanic shrubs were selected near the northern-most (farthest) edge of their distribution. Shrubs were selected deliberately within each region to cover the range of shrub sizes present in the area.

Shrub ‘island’ area (volume) was quantified by measuring the height and diameter of each shrub and calculating the shrub’s volume using the equation for a circular cone, \[ V = \frac{\pi r^2 h}{3} \] (Ludwig et al., 1975). Shrub ‘island’ distances to the ‘continent’ were measured using GPS locations, and calculating the nearest distance to the ‘continental’ boundary. The boundary was subjectively defined as the estimated line that separated the high-density, homogenous creosotebush stands (i.e. ‘continent’) from the lower-density, grass-dominated stands. Shrub isolation was quantified by (1) averaging the distances to the nearest four creosotebushes surrounding each sampled shrub, and (2) by measuring local shrub densities by counting the number of creosotebushes within a 5, 50, and
Figure 1. Study site on the Sevilleta National Wildlife Refuge, New Mexico, showing regions of (a) ‘continental’, high-density shrubs, (b) ‘archipelago’, medium-density shrubs, and (c) ‘oceanic’ isolated shrubs.
100 m radius centered on the sampled shrub for ‘continental,’ ‘archipelago’ and ‘oceanic’ shrubs, respectively. Shrub distances from one another were measured using a 100-m tape, or a laser range finder when distances between shrubs exceeded 100 meters.

Each shrub’s arthropod assemblage was collected with a pyrethrum-based insecticide (CB-80 Extra, TM Waterbury Companies Inc., Waterbury, CT, U.S.A.). A standard bed sheet was placed beneath each shrub to collect fallen arthropods. A PVC pipe-framed cube, wrapped in heavy plastic sheets, was then placed over the shrub, with the ground sheet tucked tightly against the cube’s lower frame to prevent arthropods from escaping. The enclosed shrub was then fogged with the insecticide and re-fogged after 10 minutes. After another five minutes, the shrub’s branches were beaten with a PVC rod as a means of knocking arthropods from the shrub onto the sheet. The sheet’s contents were then carefully gathered, placed in plastic bags within an ice-packed cooler, and transported to the laboratory for sorting and analysis. All samples were collected in the mornings between 05:00 and 11:00 h.

The initial (20–28 July) sampling of the shrubs effectively resulted in a total extinction of the resident arthropods; this permitted us to test for recolonization patterns predicted by Island Biogeographic Theory. To examine the recolonization patterns, we repeated the insecticide treatment on these same shrubs & 2 wk after the first sample (5–6 August), and compared the results of this second sample to the patterns observed in the initial sample.

Arthropod samples were sorted, identified to species, and counted using 10 × -40 × dissecting microscopes in the laboratory. Voucher specimens of all taxa were deposited in the University of New Mexico’s Museum of Southwestern Biology, Division of Arthropods.

Classification of collected arthropods

Collected arthropods were classified into three categories based on their known (or unknown) association with creosotebush.

The first category included species considered as creosotebush specialists. They were designated as such based on literature (e.g. Hurd & Lindsey, 1975) and the results of a separate project being conducted on the Sevilleta NWR (R. Parmenter, unpublished data). In this latter study, plant-dwelling arthropod communities were sampled from grassland, shrubland and woodland habitats across the Sevilleta NWR. Specialists of creosotebush were defined as those species which had been found exclusively on or beneath creosotebushes and in absence from the other plant species.

The second category included species that were considered generalists, i.e. those that relied on generic vegetative architecture for predation (e.g. spiders and mantids), those that were known to be herbivores of other vegetation (e.g. the grasshopper, Melanoplus arizonae, on area grasses), and those whose habits were understood well enough to confidently infer their lack of dependence on creosotebush (e.g. robber flies Asilidae).

The third category included arthropods whose association with creosotebush was uncertain, due to their habits being largely unknown. Many within this group were parasitoid wasps with unknown hosts that may or may not be creosotebush specialists. As such, they were not considered as specialists, nor included in analyses addressing specialist species.

Statistical analyses

For each ‘island’ shrub category (‘continent,’ ‘archipelago’ and ‘oceanic’), we calculated means for shrub density, distance from continent, isolation, and number of main branches extending from the base of the shrub (an index of shrub architectural
complexity), diameter, height, and volume. For the arthropods, we analysed separately the two major groups of arthropods found on the shrubs: the specialist herbivores and the generalist predators. Species lists and abundances for each shrub were tallied, and species-dominance curves were constructed. Mean abundances for specialist herbivores and generalist predator species also were calculated within each of the three categories both initially and following recolonization.

The relationships among initial and recolonized specialist herbivore populations and shrub characteristics were assessed using regression analysis. Specifically, we compared: (1) the number of specialist herbivore species per shrub to shrub volume; (2) the number of specialist herbivore species per shrub to shrub distance from the shrub ‘continent’; (3) the number of specialist herbivore species per shrub to local shrub density (shrubs m$^{-2}$); and (4) the number of specialist herbivore species per shrub to average shrub distance from its nearest four shrub neighbors. Regression analysis also was used to compare population sizes of individuals per shrub to shrub distance from the ‘continent’ both initially and following recolonization for the four dominant herbivore species. In addition, we performed a multiple regression analysis using both shrub volume and distance to ‘continent’ to determine which of these factors were most important in influencing the arthropod species richness.

The distribution of generalist predator arthropods (spiders [Araneae] and mantids [Mantodea]) for both initial and recolonized species assemblages were assessed using regression analysis as a means to compare: (1) the number of predators per shrub to shrub volume; (2) the number of predators per shrub to the number of main branches per shrub (3) the number of predators per shrub to local shrub density; (4) the number of predators per shrub to shrub distance to the ‘continent’; and (5) the number of predators per shrub to the number of specialist prey items on shrubs in ‘continental,’ ‘archipelago’ and ‘oceanic’ categories. All regression analyses were evaluated using a significance level of $p \leq 0.05$.

**Results**

*Shrub ‘island’ characteristics*

The ecotonal area of McKenzie Flats provided study sites with a wide range of shrub distributions, with creosotebush densities ranging over more than three orders of magnitude (Table 1, Fig. 1). Mean isolation measures and distances of shrub ‘islands’ to the high-density ‘continent’ also varied greatly (Table 1). However, shrub characteristics (number of branches, diameter, height and volume) were comparable in all three study regions (Table 1).

The 12 high-density ‘continental’ shrubs ranged from 0.07 to 2.22 m$^3$ in volume, and from 0.83 to 2.88 m in average distance to their nearest four creosotebush neighbors. The 12 medium-density ‘archipelago’ shrubs ranged from 0.05 to 1.88 m$^3$ in volume, from 0.15 to 0.46 km in distance to the ‘continent’, and from 6.75 to 22.5 m in average distance to their nearest four creosotebush neighbors. The 12 low-density ‘oceanic’ shrubs ranged from 0.10 to 1.17 m$^3$ in volume, from 2.92 to 3.59 km in distance to the ‘continent’, and from 55.0 to 224 m in average distance to their nearest four creosotebush neighbors (Table 1).

*Arthropod fauna*

We found 91 arthropod species in the 36 creosotebushes sampled. Twenty-one species were categorized as creosotebush specialist species, 53 as generalist species, and 17 as species of unknown relationship with creosotebush.
Table 1. Size and density characteristic of Larrea tridentata in study areas of the Sevilleta National Wildlife Refuge, New Mexico. Values are means ± standard deviation, n = 12

<table>
<thead>
<tr>
<th>Region</th>
<th>Continental</th>
<th>Archipelago</th>
<th>Oceanic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean density (shrubs/ha)</td>
<td>5900 ± 2900</td>
<td>60 ± 30</td>
<td>3 ± 1</td>
</tr>
<tr>
<td>Mean isolation* (m)</td>
<td>1.56 ± 0.53</td>
<td>12.7 ± 5.3</td>
<td>103.0 ± 65.0</td>
</tr>
<tr>
<td>Mean distance to continent (km)</td>
<td>—</td>
<td>0.30 ± 0.10</td>
<td>3.18 ± 0.25</td>
</tr>
<tr>
<td>Mean number of branches/shrub</td>
<td>15.6 ± 3.48</td>
<td>13.1 ± 3.94</td>
<td>15.5 ± 3.23</td>
</tr>
<tr>
<td>Mean shrub diameter (m)</td>
<td>1.22 ± 0.46</td>
<td>1.37 ± 0.50</td>
<td>1.18 ± 0.34</td>
</tr>
<tr>
<td>Mean shrub height (m)</td>
<td>0.94 ± 0.29</td>
<td>1.06 ± 0.32</td>
<td>0.76 ± 0.18</td>
</tr>
<tr>
<td>Mean shrub volume (m³)</td>
<td>0.48 ± 0.58</td>
<td>0.66 ± 0.56</td>
<td>0.33 ± 0.31</td>
</tr>
</tbody>
</table>

*Measured as the mean distance to the nearest four creosotebushes.

The 21 specialist species (Table 2) included four beetles (Coleoptera) representing two families, one fly (Diptera), six true bugs (Heteroptera) representing two families, seven leafhoppers (Homoptera) representing four families, and one species each of moth (Lepidoptera), grasshopper (Orthoptera), and bark lice (Psocoptera). The most abundant specialists overall were Multaris sp., Multaris cornutus (Homoptera), larval Semiothesia colorata (Lepidoptera), and Phytocoris vanduzee (Heteroptera).

The 53 generalist species included 14 beetles (Coleoptera), three flies (Diptera), three true bugs (Heteroptera), five leafhoppers (Homoptera), five ants, seven wasps (Hymenoptera), one moth (Lepidoptera), three mantids (Mantodea), two grasshoppers (Orthoptera), one walking stick (Phasmida), eight spiders (Araneae), and one mite (Acari).

The 17 species having uncertain relationships with creosotebush included three beetles (Coleoptera), six flies (Diptera), one ant and seven wasps (Hymenoptera).

Tests of Island Biogeographic Theory

We first tested the prediction that species richness of specialist herbivore arthropods was positively related to ‘island area’ (shrub volume). Regression analyses confirmed that specialist herbivore arthropod species richness was significantly positively correlated to shrub volume, both in the initial sample and after the two-week recolonization period (Fig. 2). Species richness averaged 3.2 species in the smallest shrubs (0.04–0.12 m³) and increased linearly to 10.8 species in the largest shrubs (1.16–2.21 m³) in the initial sample; richness values were smaller in the recolonized sample, but displayed a comparable pattern with increasing shrub volume (Fig. 2).

We next tested the prediction that species richness of specialist herbivores would decrease with increasing distance of the shrub ‘islands’ from the high-density shrub ‘continent.’ In the initial sample, species richness was found to be significantly negatively related to shrub distance to the high-density shrub region (Fig. 3). Species richness values in the ‘continent’ and ‘archipelago’ regions were similar, averaging 6.0–8.8 species per shrub, but declined to 5.3 species per shrub in the most distant ‘oceanic’ region. In the post-recolonization sample, a similar, though non-significant, negative slope ($r^2 = 0.08, p > 0.05$) also was observed. In contrast to the significant distance effect, we found no significant correlation between specialist herbivore arthropod species...
<table>
<thead>
<tr>
<th>Species ID. #</th>
<th>Order</th>
<th>Family</th>
<th>Species</th>
<th>Initial Continental</th>
<th>Archipago</th>
<th>Oceanic</th>
<th>Recolonized Continental</th>
<th>Archipago</th>
<th>Oceanic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Coleoptera</td>
<td>Chrysomelidae</td>
<td><em>Pachybrachis xantho lucens</em></td>
<td>1.27 ± 2.05</td>
<td>1.18 ± 1.54</td>
<td>0.64 ± 2.11</td>
<td>0.58 ± 0.79</td>
<td>0.25 ± 0.45</td>
<td>0.28 ± 0.29</td>
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<td>Chrysomelidae</td>
<td><em>Psylliodes sp.</em></td>
<td>0.18 ± 0.40</td>
<td>0.18 ± 0.40</td>
<td>—</td>
<td>2.42 ± 2.61</td>
<td>4.50 ± 3.58</td>
<td>1.08 ± 1.24</td>
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<td>Coleoptera</td>
<td>Curculionidae</td>
<td><em>Cimbroca sp.</em></td>
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<td>2.73 ± 3.50</td>
<td>0.82 ± 0.88</td>
<td>2.17 ± 1.42</td>
<td>0.17 ± 0.39</td>
<td>0.17 ± 0.58</td>
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<td>4</td>
<td>Coleoptera</td>
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<td><em>Orphryastes dunnianus</em></td>
<td>0.27 ± 0.90</td>
<td>0.27 ± 0.65</td>
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<td>0.50 ± 1.00</td>
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<tr>
<td>5</td>
<td>Diptera</td>
<td>Cecidomiidae</td>
<td><em>Asphondylia auripilia</em></td>
<td>0.18 ± 0.60</td>
<td>2.00 ± 2.53</td>
<td>1.27 ± 1.42</td>
<td>0.18 ± 1.98</td>
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<td>6</td>
<td>Heteroptera</td>
<td>Miridae</td>
<td><em>Phytocoris migninus</em></td>
<td>0.55 ± 1.21</td>
<td>2.27 ± 2.41</td>
<td>0.73 ± 1.56</td>
<td>0.58 ± 1.44</td>
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<td>2.91 ± 6.44</td>
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<tr>
<td>8</td>
<td>Heteroptera</td>
<td>Miridae</td>
<td>Unidentified sp. 1</td>
<td>0.17 ± 0.39</td>
<td>0.08 ± 0.29</td>
<td>—</td>
<td>0.33 ± 0.49</td>
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<tr>
<td>9</td>
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<td>0.83 ± 1.53</td>
<td>1.92 ± 2.31</td>
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<td>0.50 ± 0.67</td>
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<td>0.24 ± 0.45</td>
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<td>0.25 ± 0.45</td>
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<td>0.17 ± 0.39</td>
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<td>0.17 ± 0.58</td>
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<tr>
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<td>Unidentified sp. 3</td>
<td>0.17 ± 0.58</td>
<td>0.17 ± 0.39</td>
<td>—</td>
<td>0.08 ± 0.29</td>
<td>0.17 ± 0.58</td>
<td>—</td>
</tr>
<tr>
<td>16</td>
<td>Homoptera</td>
<td>Membracidae</td>
<td><em>Muitaris cornutus</em></td>
<td>2.83 ± 5.08</td>
<td>17.1 ± 8.15</td>
<td>2.33 ± 5.16</td>
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<td>0.58 ± 1.16</td>
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<tr>
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<td>Membracidae</td>
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<td>41.8 ± 41.1</td>
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<td>17.0 ± 9.72</td>
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<td>Homoptera</td>
<td>Psyllidae</td>
<td><em>Heteropsylla texana</em></td>
<td>0.17 ± 0.39</td>
<td>1.67 ± 3.06</td>
<td>—</td>
<td>0.08 ± 0.29</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>19</td>
<td>Lepidoptera</td>
<td>Geometridae</td>
<td><em>Semiothisa colorata</em></td>
<td>3.17 ± 2.59</td>
<td>12.4 ± 13.7</td>
<td>8.75 ± 8.72</td>
<td>3.17 ± 2.59</td>
<td>—</td>
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</tr>
<tr>
<td>20</td>
<td>Orthoptera</td>
<td>Acrididae</td>
<td><em>Bootettix argentatus</em></td>
<td>0.25 ± 0.62</td>
<td>0.17 ± 0.39</td>
<td>0.08 ± 0.29</td>
<td>0.50 ± 0.67</td>
<td>0.17 ± 0.39</td>
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<tr>
<td>21</td>
<td>Psocoptera</td>
<td>Unknown</td>
<td>Unidentified sp. 1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.25 ± 0.45</td>
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</table>
richness and ‘island isolation,’ as measured by either local creosotebush density ($r^2 = 0.021, p > 0.05$) or to the average distance to the shrubs’ nearest four creosotebush neighbors ($r^2 = 0.08, p > 0.05$).

The results of the multiple regression analysis produced a significant result with the combined model of shrub volume and distance influencing species richness in the initial sample ($R^2 = 0.36, p < 0.01$); within this combined model, the distance between the ‘island’ and the ‘continent’ proved most important ($R^2 = 0.26, p < 0.01$), whereas ‘island’ size (shrub volume) contributed a non-significant amount to the regression ($R^2 = 0.09, p < 0.1$). For the recolonized arthropod samples, only shrub volume proved to contribute a significant portion to the model ($R^2 = 0.28, p < 0.01$).

The species-dominance relationship of specialist herbivore species among all shrubs was disrupted by the ‘extinction’ sampling treatment (Fig. 4(a,b)). Following ‘extinction’ and recolonization, the overall totals of specialists were lower and the rank of individual species altered. Although the most abundant species (Multaris sp.) remained so following the second sampling effort, larvae of Semiothesia colorata, initially having the third highest individual species total, were absent from the recolonized assemblage.

We also tested the hypothesis that the abundances of the dominant herbivore species would be influenced by distances between shrub ‘islands’ and the shrub ‘continent.’ Regression analyses showed significantly smaller initial populations of Multaris sp., Phytocoris vanduzee, and Multaris cornutus on more distant shrub ‘islands’ (Fig. 5(a,c,d)), whereas that of Semiothesia colorata exhibited no significant relationship (Fig. 5(b)). Following the recolonization period, population sizes of Multaris sp., Phytocoris vanduzee, and Multaris cornutus again were significantly negatively related to ‘island’ distance from the shrub ‘continent’ (Fig. 5(a,c,d)); Semiothesia colorata larvae failed to recolonize at all, although adult moths of this species may have laid eggs that had not yet hatched (Fig. 5(b)).

In examining the patterns of generalist predator populations on shrubs, we found that, as with the specialist herbivores, predator population size exhibited a significantly positive relationship to shrub volume both initially and following recolonization (Fig. 6). Similarly, predator abundance displayed a significantly positive relationship to the number of main branches per shrub (an index to architectural complexity; Fig. 7). We also found that initial and recolonized populations were significantly negatively related to local shrub density (Fig. 8), but not significantly correlated to shrub ‘island’ distance to the ‘continent’ ($r = 0.00, p > 0.05$). Finally, in relating predator and prey abundances on shrub islands, the abundances of predators were positively associated with specialist herbivore prey abundances (Fig. 9), with ‘continental’ and ‘oceanic’ island populations exhibiting the strongest relationships; however, the slopes of the three regressions did not differ significantly.

**Discussion**

*The species richness–island area relationship*

In Island Biogeographic Theory, the species richness–island area hypothesis predicts that larger areas of suitable habitat are able to support a larger number of species and individuals of those species. This relationship is well documented for many taxa (Brown & Lomolino, 1998), including arthropods (e.g. Rukke, 2000; van Dongen et al., 1994). As such, this relationship has justly been described as ‘one of community ecology’s few genuine laws’ (Schoener, 1976: 629). Our results indicate that a similar pattern exists within this desert shrubland-grassland ecotone. We found that larger creosotebushes supported larger numbers of specialist herbivore species and, after an ‘extinction’ event, subsequently experienced higher rates of immigration (Fig. 2).
Figure 2. Semi-log relationship between the species richness of specialist herbivore arthropods on creosotebushes and shrub 'island area' (volume). (a) 'Initial' represents the first sample collected, and (b) 'Recolonized' represents the sample taken two wk after the initial defaunation.

One explanation for the pattern is that there is a greater abundance of available resources to specialist herbivores on larger shrubs thereby increasing the individual shrub’s carrying capacity (Marques et al., 2000). Another explanation is that immigration to a particular shrub is positively related to shrub size, and is probably a consequence of what Gilpin & Diamond (1976) described as the ‘target area effect.’ Their proposition asserts that larger island size increases the chance of attracting an active immigrant based upon the fact that the island is more easily detected. Our observations are analogous to those of Rey (1981), who similarly documented the relationship between the size of defaunated Spartina islands and their subsequent recolonization of arthropods.
The species richness–island distance relationship

Our data indicate that a negative relationship exists between specialist herbivore species richness and shrub ‘island’ distance to the high-density ‘continent’ prior to defaunation (Fig. 3). Similar results are well evidenced in the literature (e.g. Diamond, 1972).

In addition to there being fewer specialist herbivorous species on distant creosotebush ‘islands’, we also found that the dominant herbivore species exhibited smaller population sizes per shrub as distance from the ‘continent’ increased (Fig. 5). Combining these two

Figure 3. Semi-log relationship between the species richness of specialist herbivore arthropods on creosotebushes and shrub ‘island’ distance from the defined ‘continent.’

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Figure 4. Arthropod species-dominance histograms of specialist herbivore arthropod species from all sampled creosotebushes: (a) ‘Initial’ sample species composition, ranking species left to right by their respective total number of individuals present; (b) ‘Recolonized’ species maintaining the order of species rank established in (a). The ‘ID #’ corresponds to the species identification number listed in Table 2.
Figure 5. Semi-log relationship between the population sizes of dominant specialist herbivore arthropod species on creosotebushes and shrub ‘island’ distance from the defined ‘continent’. Initial values (●) and values following recolonization (▲) of: (a) *Multaris* sp.; (b) *Semiothesia colorata*; (c) *Phytocoris vanduzeei*; and (d) *Multaris cornutus*.

Observations, we suggest that ‘oceanic’ shrubs may be subjected to lighter herbivore pressures from specialist arthropod species, which may favor their survival as they ‘invade’ a grassland habitat. The colonization of new habitats (in this case, grasslands) exposes the creosotebushes to new biotic and abiotic pressures, including potential competition for resources (e.g. water, nutrients) from the resident vegetation. The lower herbivore load of these colonizing shrubs may confer some compensatory benefit, thereby enhancing their ability to successfully establish and reproduce in the new environment. Ultimately, this process would promote shrub encroachment into the adjacent grasslands and perhaps advance the rate of desertification.

The species richness–island isolation relationship

The species richness–island isolation relationship has yielded a lesser body of conclusive evidence. This may be the result of problems quantifying island isolation and/or the
dispersal abilities of immigrants (Brown & Lomolino, 1998). The basis of the relationship is dependent on the assumptions that (1) the dispersal abilities of potential immigrant species are variable and limited, and (2) islands with higher degrees of isolation are more difficult for dispersers to detect and successfully colonize (Wiens, 1997).

While our results pertaining to species richness and shrub ‘island’ distance to the shrub ‘continent’ supported Island Biogeographic Theory (Fig. 3), our results concerning species richness and shrub ‘island’ isolation (densities or nearest neighbor distances) were not consistent with theoretical predictions. It may be that shrub ‘isolation’ (density, or average distance to neighbors) under these circumstances is relatively unimportant to these particular arthropod species, and that original species richness and that following immigration is solely related to shrub distance from dense, expansive patches of creosotebush (i.e. ‘continent’). Altogether, our findings illustrate some of the complications associated with examining the species richness–island isolation relationship.

The realization that variables other than island isolation can influence species distributions in island systems has proven to be essential in characterizing island biogeography (Brown & Lomolino, 2000). Chief among these variables is species-specific vagility. Earlier studies have demonstrated that dispersal ability often affects the distribution of species in island systems (e.g. Lomolino, 1984) by skewing anticipated island
Figure 7. Relationship between the population sizes of generalist predator arthropods (spiders and mantids) on creosotebushes and shrub architectural complexity (numbers of major branches). (a) ‘Initial’ represents the first sample collected, and (b) ‘Recolonized’ represents the sample taken two weeks after the initial defaunation.

population sizes (MacArthur, 1965) or wholly preventing certain species from establishing on islands (Abbot & Black, 1980).

In our study, we found that, of the four dominant herbivore species, only the larvae (inchworms) of the moth, *Semiothesia colorata*, failed to recolonize the creosotebushes following defaunation (Table 2, Fig. 5(b)), although adult moths may have visited the shrubs undetected and laid additional eggs. The other species, all strong fliers, were able to successfully recolonize even the most distant and isolated shrubs. In contrast, the creosotebush grasshopper, *Boettettixargentatus*, a relatively weak flier, was able to recolonize the ‘archipelago’ shrubs, but not the distant ‘oceanic’ shrubs (Table 2). Clearly, in the shrubland-grassland ecotone of our study site, species-specific dispersal ability was a critical determinant of recolonization success. These observations were similar to those of Spiller et al. (1998), who concluded that the poor dispersal capabilities of lizards largely determined their absence from suitable islands in the Bahamas following a catastrophic hurricane in 1996.
Figure 8. Semi-log relationship between the population sizes of general predator arthropods on creosotebushes and shrub ‘island’ density. (a) ‘Initial’ represents the first sample collected, and (b) ‘recolonized’ represents the sample taken two weeks after the initial defaunation.

**Predator-prey patterns**

The arthropod predators (spiders and mantids) found on the shrubs were habitat generalists that would be common in the surrounding grassland matrix as well as on creosotebushes. In particular, spiders used the shrubs during foraging because the architectural complexity of the shrub microhabitat was conducive to the ambush hunting strategy of many species. Shrubs with greater architectural complexity tend to support greater spider species richness and abundance (e.g. Robinson, 1981). In our study, predator abundances on shrubs were shown to be significantly positively related to the number of main branches per shrub and shrub volume. As such, the presence of an isolated shrub in a grassland matrix provided predators with an ‘island’ of unique habitat based on architectural attributes, and may therefore attract a higher density of predators from the surrounding habitat.
Our observations of predator patterns on shrub ‘islands’ were consistent with this concept, as we found that predators on isolated (low-density) creosotebushes in the ‘archipelago’ and ‘oceanic’ sites were significantly more abundant than on ‘continental’ shrubs (Fig. 8). This pattern indicated a threshold effect of shrub density on predator abundance, in that a shrub ‘island’ in a grassland ‘sea’ accrued greater generalist predator populations regardless of how far it was from the shrub ‘continent.’

Did the increased density of predators on ‘island’ shrubs influence the abundances of the herbivore prey populations? In general, larger shrub ‘islands’ supported greater populations of both predators and herbivore prey (Figs 2, 6), and predator-prey abundances on the shrubs were significantly associated (Fig. 9). Our data showed that the population sizes of the dominant herbivore specialist species were significantly smaller on ‘oceanic’ shrub islands (Fig. 5), while predator abundances were significantly higher (Fig. 8). These observations were consistent with a ‘prey-suppression’ effect by predator activities. We caution, however, that our broad categories of predator and prey were not sufficiently detailed to elucidate the interactions of particular predator and prey species, and that these coarse classifications may have masked the actual relationships within this shrub-arthropod community. Future studies on the natural history of these arthropods will presumably allow more detailed assessments of the predators’ role in regulating the specialist herbivore population sizes.

**Limitations of a ‘shrub island’ model**

While our overall results were consistent with the species richness-island area relationship, and with the species richness-island distance relationship, the desert ‘shrub island’ analogy clearly had several limitations. First, instead of functioning as inert targets for dispersing herbivorous arthropods, desert shrubs produce chemical cues to which arthropods may respond. It is known that many plants release pheromones or aromatic organic compounds that arthropods use as navigational aides (e.g. Loughrin *et al.*, 1996). By directing insect movement, these cues increase the probability that an individual arthropod will successfully locate a distant host plant. This may reduce the stochastic aspect of long-distance dispersal, thereby disrupting the predicted random...
immigration patterns. In true oceanic island systems, high wind conditions and much larger distances make it unlikely that such cues would be important for dispersing arthropods.

Second, our desert shrub ‘island’ model differs from that of true oceanic islands in that grassland areas between creosotebushes are not necessarily lethal to dispersing arthropods (as would be open water). This allows immigrants to stop and rest en route to distant shrub ‘islands’ without compromising their immigration success. Thus, these two functional differences in ‘island’ models may explain some of the inconsistencies we found with the species richness–island isolation relationship.

Summary

In its entirety, our study is in accordance with the species richness–island area and the species richness–island distance relationships of the Island Biogeographic Theory. We found that species richness of specialist arthropod herbivores on creosotebush ‘islands’ was correlated with shrub volume (‘island’ area), and that shrub ‘island’ distance to the shrub ‘continent’ was significantly negatively related to shrub species richness. Based on these observations, and knowledge of the species-specific dispersal capabilities of the creosotebush arthropods, we suggest that shrub ‘island’ size and distance from high-density shrub habitats, along with the dispersal ability of individual arthropod species, largely determines shrub-dwelling arthropod distribution patterns across this desert landscape. Generalist predator populations displayed positive relationships with shrub size and architectural complexity, and predator abundances on shrubs were positively correlated with prey abundances. The role of predators in influencing the distributions and abundances of their herbivorous prey species on shrub ‘islands’ may be important, although additional studies will be required to attain a more detailed understanding of the interspecific relationships within this shrub-arthropod community.

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References


