

Article

Effects of Peri-Urbanization on Coastal Sage Scrub Ant Species in Baja California

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Abstract: Increasing urbanization on the Baja California Peninsula threatens ant diversity. Reductions in ant species diminish ecosystem services provided to semiarid coastal scrub areas. Peri-urban areas in particular are at high risk of reductions in ant biodiversity due to development. To document and evaluate ant species diversity and richness in a rapidly developing area, nine sites were sampled within areas of coastal sage scrub (CSS) encircling the urban periphery of Ensenada, Baja California. Forty species and 17 genera of ants were collected, only one of which was non-native. Although the sampled area represents less than 1% of the peninsula and 3% of the State of Baja California, approximately one-third of the total species recorded for the peninsula and state were collected. Environmental variables (compass orientation, slope, and vegetation cover) were not significant determinants of species richness. Sandy soils were associated with the highest species abundance, richness, and functional diversity of feeding guilds. Despite limitations, our results present a historically significant snapshot of ant diversity in the sage scrub areas surrounding Ensenada. Sandy regions of semiarid coastal scrub are prime conservation management areas as they support the greatest functional diversity and have the highest potential to supply environmental services to the surrounding CSS ecosystem.

Keywords: biodiversity conservation; Baja California; coastal sage scrub ecosystems; ecosystem services; family Formicidae



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1. Introduction

Urban expansion is inevitably accompanied by pressure to convert natural areas into space for agriculture, livestock, and industrialization [1]. Unfortunately, urbanization often comes at the expense of biodiversity and contiguous areas of vegetation cover. Increasing habitat fragmentation can drive shifts in species richness, composition, and functional diversity [2], ultimately impacting biodiversity and ecosystem functions [3,4]. This is particularly concerning as urbanization is a global phenomenon; it is predicted that 2.5 billion additional people will occupy cities by 2050 [5].

Development strongly influences vegetation in newly urbanized desert ecosystems, often leading to the dispersal of new species and the elimination of plant cover in some areas [6]. This is an important consideration for Mexico in that arid and semiarid ecosystems represent about 60% of the national territory, and these arid areas are home to some 6000 species of plants [7]. One particular form of semiarid vegetation, coastal sage scrub (CSS), is characteristic of the lowland and middle elevations of the coastal Pacific Mediterranean Climate Zone that encompasses the southern portions of California and northwest Baja California [8,9]. The CSS ecosystem is a biodiversity hotspot that supports high plant species richness and endemism [10,11], including at least 60 plants and thirty animal taxa considered rare [12].

The ecosystem services ants provide are critical in grasslands [13,14], where they can also be indicators of habitat restoration progress [14,15]. Some ant species, for example, are predators that suppress pest species [16,17]; others are pollinators [18,19] and transporters of soil nutrients [13]. Ants assist in the decomposition of organic matter and recycling of nutrients [20] and are one of the most common invertebrate seed dispersers [21,22]. In Mediterranean areas subject to natural fire regimes, ants also play an essential role in seed dispersal after fire [23,24]. The sensitivity of ants to environmental disturbance and land management techniques, and their integral role in ecosystem regulation, makes them ideal for exploring hypotheses about biodiversity and land use changes [25].

Regions of CSS are under severe pressure from urban expansion, frequent fires [26], and drought [10–12]. In Baja California, CSS has decreased by as much as 90% in some locations [27]. Some studies of the effects of this intense urbanization process on the vegetation in northwestern Baja California exist [27].

However, there is limited information on its effects on fauna [28], particularly on the ants present in these environments [29]. Urbanization drives physical and chemical changes in the soil, increasing the isolation of plant and animal populations, disturbing biotic interactions, reducing plant cover, and increasing the introduction of non-native species, all of which profoundly modify the CSS ecosystem [30,31]. Climate change will undoubtedly exacerbate these changes [26].

Basic research on the specific ant species found on the Baja peninsula is extremely scarce, with most work dating from before 2002. Johnson and Ward [32] presented the first exhaustive list of ant species for the peninsula based on a review of historical records, museums, and literature. However, they acknowledged that the list of 176 species of ants their survey recorded was far from complete given that Mexico is home to a high diversity of ant species (407 species; [33]) and a substantial percentage of the 580 known species in the Nearctic Region of North America [34]. Many studies address the role ants play in providing services to semiarid ecosystems. Some also emphasize the importance of Mediterranean Climate Zone ecosystems such as CSS as biodiversity hotspots. However, an in depth literature review in 2010 found only 14 publications that even mention ants in the Baja Peninsula [29]. Only three additional papers on this topic have been published since 2013 [35,36]. It is, therefore, important to document the ant assemblages in this unique region and their relationships to the environments they inhabit. In this paper, we characterize the assemblages of ants present in the peri-urban area of the city of Ensenada, a sensitive region poised for increased urbanization [31]. We specifically ask what geographical and ecological components of the local CSS ecosystem are associated with high ant species richness and functional diversity. Our goal is to better understand the biotic and abiotic factors governing the presence of distinct ant species in this unique and understudied arid ecosystem.

2. Materials and Methods

2.1. Study Area

The Baja California peninsula has temperate Mediterranean-type vegetation in the northwest of the peninsula and tropical vegetation in the Cape Region of the extreme south, with a long desert transition between the two areas. The Mediterranean Climate Zone of California and northwestern Baja California is recognized as a global biodiversity hotspot, but within this ecozone, CSS areas are threatened by urban sprawl on both sides of the border [1,27,37,38].

The state of Baja California is a paradigmatic example of urban expansion. From 1970 to 2005, the local population tripled, reaching almost 3 million inhabitants, of which 93% reside in urban areas. Most of this population (64%) is concentrated in the urban corridor extending over 100 km from Los Angeles, CA, to Ensenada, Baja California. Ensenada (31°52' N; 116°37' W) is Mexico's fourth largest city, with a growing population of almost half a million people [39].

2.2. Sampling Methods

Nine sampling sites were selected to encircle the entire arc of the Ensenada urban periphery (Figure 1). At each site, two concentric sampling plots were established to measure ecological variables at two different scales (Figure 2), according to the methods of Dauber et al. [40]. Each plot had a core area of 120 m radius (4.5 ha) with a surrounding 80 m wide (8 ha) buffer. The percentage of vegetation cover for each site was calculated from Google Earth images at a scale of 1:4000. The core sampling plot area was calculated at a scale of 1:1500, and the surrounding buffer was calculated at a scale of 1:2500. Cover percentage was further characterized within the concentric sample plots (core and buffer) as being shrubby (S, woody plants with multiple rigid stems arising from the base), herbaceous (H, non-woody plants with flexible stems, e.g., grasses, forbs, etc.), or bare soil (B). The slope (degrees), orientation (compass point), and elevation (meters above mean sea level, mamsl) were calculated for each site based on a digital elevation model of Ensenada, B.C., generated with the programs Idrisi (© 2021 Clark Labs) and ArcView 3.2 (ESRI (1999) using information from INEGI (2010) (charts H11B11-12, H11B21-22). Three distinct soil textures were identified for this study. These followed the United States Department of Agriculture (USDA) Unified Soil Classification (USC) system and were designated as sandy soil (S, particle sizes from 0.075 to 4.75 mm), rocky/gravel (R, particle sizes from 4.75 to 75 mm), and compact clay (C, particle sizes less than 0.075 mm), based on the degree of porosity and compaction.

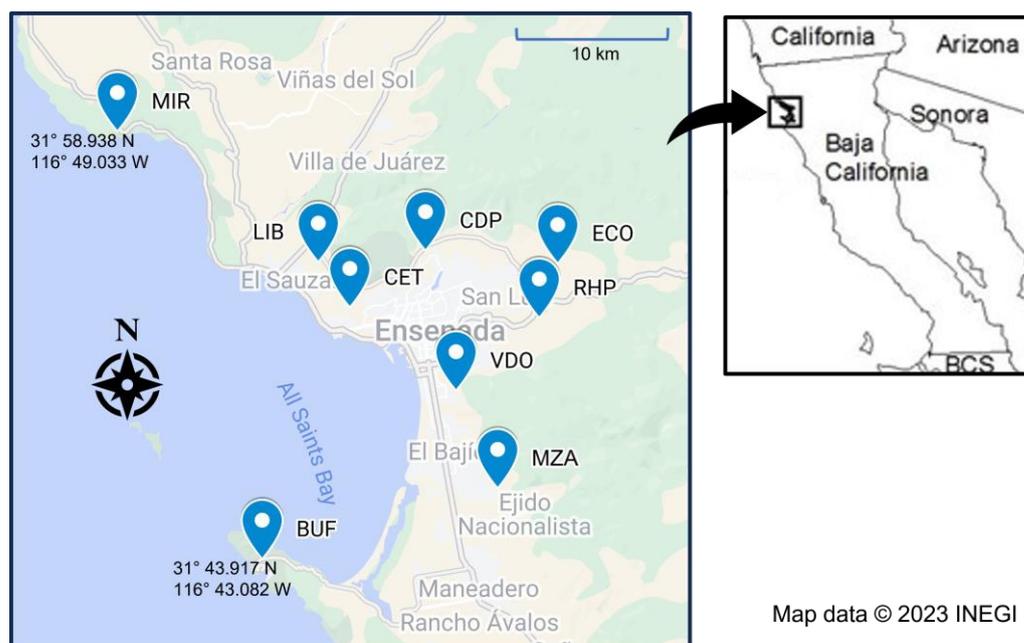


Figure 1. Study area in urban periphery of Ensenada, Baja California. Nine sampling sites (blue markers) were located in areas of coastal sage scrub to encompass the entire arc of the city of Ensenada.

Ant species data were collected from July through October of 2009 according to a modified version of the ALL protocol described by Agnosti and Alonso [41] using pitfall traps, baited traps, and manual collections. This protocol was adopted as there is no single best method to sample ground-dwelling ant fauna. Given the paucity of data for ant species in the CSS of the Baja Peninsula, multiple methods and greater effort were necessary to obtain a thorough inventory of species in the area.

Within the sampling area of each site (Figure 2), three 200 m long linear transects were delineated, separated by 60 m. Five pitfall traps were placed in each transect separated by 40 m, for a total of 135 pitfall traps (9 sites × 3 transects × 5 traps). Traps consisted of 12 cm diameter plastic cups at ground level, filled with a detergent and water solution up to 75% of the total volume of the cup. The traps remained in place for seven days before

being removed. The contents of each trap were filtered into plastic bags (whirl-pack® or Ziploc) and preserved with 75% ethanol.

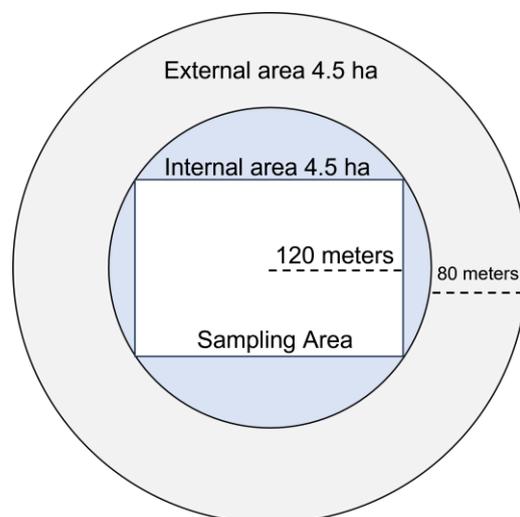


Figure 2. Sampling areas (core and buffer) for ecological variables were established for each study site. Each internal core had a radius of 120 m (4.5 ha) with an external buffer area of 80 m (8 ha) and a total area of 12.5 hectares.

Additionally, four 100 m linear transects were established at each sampling site. The transects were arranged 10 m apart and with 10 baited traps per transect separated from each other by 10 m. In each transect, four different types of bait (tuna, peanut butter, sweet cookie crumbs, and sausage) were placed in combination. In total, 360 bait traps were established (9 sites \times 4 transects/site \times 10 traps/transect), which remained in place for one hour.

Finally, manual collections augmented the standardized transect trapping methods. This was necessary to record ants that could not be trapped due to unusual and highly specific feeding and foraging habits (e.g., predatory species of the genera *Myrmecocystus*, *Pseudomyrmex*, etc.). In an area of approximately 25 m², two people examined the soil and searched under rocks, decomposing logs, flowers, and fruits at each sampling site for one hour. Individual ants were collected employing a mouth aspirator. In total, 18 person-hours were invested (9 sites \times 2 people \times 1 h). The collected material is deposited in the Arthropod Museum of the Ensenada Center for Scientific Research and Higher Education (CICESE), Ensenada, Baja California.

2.3. Data Analysis

Ant species identification data were pooled and analyzed by sampling site. Statistical analyses were conducted using the programs FDiversity [42] and R [43]. Species evenness, diversity, density ($J = H/\log(S)$, where H = is derived from the Shannon Wiener index, and S = total number of species in the habitat), and functional diversity (Rao's Q [44]) were calculated for each sample site using feeding guild and abundance as traits (FDiversity). GLM (for normally distributed species abundance) and Kruskal–Wallis (for non-normal distributions of species richness and diversity) analyses were used to explore the response of ant species to the biological and physical independent variables (R, stats package). Significance was set at $\alpha = 0.05$ for all parametric analyses. Canonical Correspondence Analysis (CCA; R, vegan package) was used to identify the biological and environmental factors influencing variation in ant species abundance and richness. Species abundance and richness were the response variables in the model. Soil type, vegetation type, elevation, site orientation, and degrees of incline of site were explanatory variables. Feeding guilds were included as a proxy biological constraint as they are reflective of resource availability, physical habitat structure, and disturbance. Cluster analysis (based on Euclidean distance,

where N = total number of species, and Si1 and Si2 = abundance of species in sample 1 and 2, respectively, and using Ward's linkage method; R, cluster package) was used to confirm the CCA analysis and to further explore similarities between sites. Together, these analyses allowed the exploration of the patterns and relationships between diversity measures and ecological explanatory variables for each site (R, cluster and vegan packages).

3. Results

3.1. Species Abundance across Sites

Overall, 40 species belonging to 17 genera of 5 subfamilies were recorded in five feeding guilds across the nine sampling sites (Table 1). Two species, *Brachymyrmex* sp.1 and *Solenopsis carolinensis*, are new records for the Baja California peninsula [45]. The taxonomic distribution of species between subfamilies was similar to that found by Johnson and Ward [32] for the whole peninsula. The subfamilies with the highest number of species were Myrmicinae (18 species) and Formicinae (14 species); Dolichoderinae presented a moderate number of species (6); and two subfamilies, Ecitoninae and Pseudomyrmecinae, were only represented by one species. No species of the Ponerinae and Cerapachyinae subfamilies were found.

Table 1. List of species recorded from the peri-urban area of Ensenada, Baja California, Mexico compared with distributions in other regions. BC: State of Baja California; BCS: State of Baja California Sur; CA: California; AZ: Arizona; SON: Sonora [35]; CHI: Chihuahua; TEH: Tehuacán. (*) designates new records. Only *L. humile* was registered as an introduced species for the Baja California Peninsula. Food guilds: Generalists (G), nectarivores (N), predators (D), granivores (Gr), and harvesters (C). Bold letters indicate subfamilies.

SPECIES	BC	BCS	CA	AZ	SON	CHI	TEH
Dolichoderinae							
<i>Dorymyrmex bicolor</i> Wheeler, 1906 (G)	x	x	x	x	x		
<i>Dorymyrmex insanus</i> Buckley, 1866 (G)	x	x	x	x	x	x	x
<i>Forelius mccooki</i> McCook, 1880 (N)	x	x	x	x	x		x
<i>Forelius pruinosus</i> Roger, 1863 (N)	x	x	x	x	x		
<i>Linepithema humile</i> Mayr, 1868 (G)	x		x	x			
<i>Tapinoma sessile</i> Say, 1836 (N)	x		x	x			
Ecitoninae							
<i>Neivamyrmex nigrescens</i> Cresson, 1872 (D)	x		x				
Formicinae							
* <i>Brachymyrmex</i> sp.1 nd. Mayr, 1868 (G)							
<i>Camponotus clarithorax</i> Creighton, 1950 (G)	x	x	x				
<i>Camponotus dumetorum</i> Wheeler, 1910 (G)	x		x				
<i>Camponotus hyatti</i> Emery, 1893 (G)	x	x	x	x			
<i>Camponotus festinatus</i> Buckley, 1866 (G)	x	x	x	x	x		x
<i>Camponotus semitestaceus</i> Snelling, 1970 (G)	x		x	x			
<i>Camponotus vicinus</i> Mayr, 1870 (G)	x		x	x			
<i>Camponotus</i> sp. BCA-2 Mayr, 1861 (G)	x		x				
<i>Camponotus</i> sp. BCA-3 Mayr, 1861 (G)	x		x				
<i>Formica francoeuri</i> Bolton, 1995 (G)	x		x				
<i>Formica moki</i> Wheeler, 1906 (G)	x		x	x			
<i>Myrmecocystus mimicus</i> Wheeler, 1908 (N)	x	x	x	x	x		
<i>Myrmecocystus testaceus</i> Emery, 1893 (N)	x		x				
<i>Myrmecocystus wheeleri</i> Snelling, 1971 (N)	x		x				
Myrmicinae							
<i>Crematogaster californica</i> Wheeler, 1919 (N)	x	x	x	x	x		
<i>Monomorium ergatogyna</i> Wheeler, 1904 (N)	x	x	x	x	x		
<i>Pheidole californica</i> Mayr, 1870 (G)	x		x				
<i>Pheidole clementensis</i> Gregg, 1969 (G)	x		x				
<i>Pheidole hyatti</i> Emery, 1895 (G)	x	x	x	x	x	x	

Table 1. Cont.

SPECIES	BC	BCS	CA	AZ	SON	CHI	TEH
<i>Pheidole pilifera</i> Roger, 1863 (G)	x		x				
<i>Pheidole vistana</i> Forel, 1914 (G)	x	x	x	x	x		
<i>Pogonomyrmex californicus</i> Buckley, 1867 (Gr)	x	x	x	x	x		
<i>Pogonomyrmex montanus</i> MacKay, 1980 (Gr)	x		x				
<i>Solenopsis amblychila</i> Wheeler, 1915 (G)	x	x	x	x	x		
* <i>Solenopsis carolinensis</i> Forel 1901 (G)							
<i>Solenopsis molesta</i> Say, 1836 (G)	x	x	x	x	x		
<i>Solenopsis xyloni</i> McCook, 1880 (G)	x	x	x	x	x		x
<i>Temnothorax andrei</i> Emery, 1895 (G)	x	x	x	x			
* <i>Temnothorax</i> sp.1 Mayr, 1861 (G)							
<i>Temnothorax</i> sp. BCA-9 Mayr, 1861 (G)	x	x	x				
<i>Veromessor andrei</i> Mayr, 1886 (C)	x		x				
<i>Veromessor stoddardi</i> Emery, 1895 (C)	x		x				
Pseudomyrmecinae							
<i>Pseudomyrmex apache</i> Creighton, 1953 (N)	x	x	x	x	x		

In the pitfall traps, 8813 individuals corresponding to 39 of the 40 species were recorded. In bait traps with a similar number of individuals (7766), only 15 species were recorded (37% of the total). One species, *Forelius pruinosus*, was only recorded in baited traps. With an effort of 18 h per person, manual collection returned only 158 individuals belonging to nine species (22% of the total).

The four most abundant species (*Crematogaster californica*, *Pheidole vistana*, *Solenopsis xyloni*, and *Temnothorax andrei*), all of which are native to this region [45], were collected in pitfall traps at all nine sites. The first two species were the most abundant in terms of presence (found in 115 and 109, respectively, of the 135 traps placed) and in individuals (1341 and 2368, respectively; 42% of the total). In baited traps, *C. californica* and *P. vistana* were also frequently found at a number of sites (9 and 4, respectively) and traps (24 and 17, respectively, of the 360 traps placed); however, *Dorymyrmex bicolor* and *Forelius mccooki* were the most abundant in terms of the number of individuals (1979 and 4037, respectively; 77% of the total), even though they were only present in one site each.

Of the least common species, most (65% of the total) were found only in three or fewer sites. Nine species were present in a single site, of which only three or fewer individuals were collected (*Myrmecocystus wheeleri*, *Camponotus* BCA-3, *Linepithema humile*; *Veromessor stoddardi*, *Pseudomyrmex apache*, *Brachymyrmex* sp.1, *Temnothorax* sp.1 and *Pogonomyrmex californicus*). One non-native species was recorded in only one of the nine sampled sites, the Argentine ant (*Linepithema humile*). None of the 45 species that Johnson and Ward considered endemic to the Baja California peninsula were found. Of the 37 remaining native species found, all are also present in the state of California [32,45].

3.2. Distribution of Feeding Guilds

Of the 40 species identified, 26 were generalists (65% of all species), 9 were nectivores (23%), 2 were granivores (5%), 2 were harvesters (4%), and 1 was predatory (3%). The relative abundance of individuals within feeding guilds varied widely across sampling sites (Figure 3). Generalists and nectar-feeding species were found at all sites. The single predatory species observed was present in highest abundance at three sites with sandy soil and found in very low abundance at two sites with rocky soil. Harvester species were found at two sites with compact soil and two sites with sandy soil, but the relative abundance of individuals in this guild on sandy sites was much higher than that observed for compact soil sites. Granivores were also found in very low abundance at one site with rocky soil and one site with sandy soil (Figure 3). The functional diversity of feeding guilds (Rao's Q) was highest for sites with sandy soil (Kruskal–Wallis, $\chi^2 = 6.16$, $p = 0.046$, $df = 2$, Table 2).

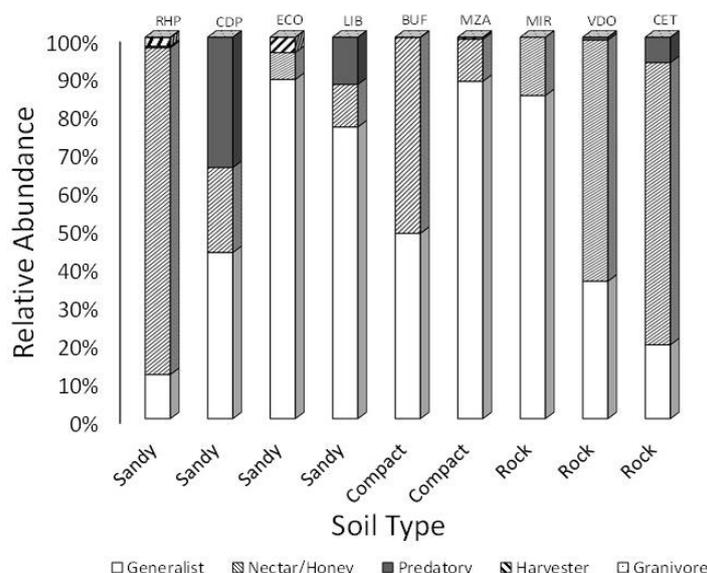


Figure 3. Relative abundance of individuals within guilds by soil type and sampling site. Doña Petra Canyon (CDP); Ecoterra (ECO); La Bufadora (BUF); Libramiento (LIB); Maneadero (MZA); Mirador (MIR); CETYS Hill (CET); Rancho Horsepower (RHP); Valle Dorado (VDO).

Table 2. Diversity indices for nine coastal sage scrub sampling sites in the peri-urban area of Ensenada, Baja California, Mexico.

PLOT	Diversity Indices						Soil	Vegetation			Slope				Elevation (mamsl)
	S	H	E	D	Rao	OR		%S	%H	%B	<10°	<20°	<30°	>31°	
RHP	22.00	0.89	0.29	0.35	0.33	S	S	4.60	61.40	34.00	80.00	19.70	0.30	0.00	273.00
ECO	20.00	1.31	0.44	0.53	0.66	S	S	8.20	58.50	33.30	86.90	13.10	0.00	0.00	338.00
CDP	20.00	1.84	0.61	0.79	0.77	E	S	19.20	60.90	19.80	33.80	66.20	0.00	0.00	143.00
MIR	15.00	2.02	0.75	0.84	0.13	N	R	1.10	72.10	26.80	56.00	20.30	12.80	10.90	142.00
VDO	15.00	1.52	0.56	0.74	0.24	W	R	7.10	92.90	0.00	39.70	55.90	4.30	0.00	117.00
BUF	17.00	1.79	0.63	0.80	0.26	S	C	1.70	72.70	25.60	55.60	38.40	6.00	0.00	102.00
CET	8.00	0.91	0.44	0.43	0.24	W	R	1.30	79.10	19.60	9.20	51.80	39.00	0.00	196.00
LIB	15.00	1.50	0.55	0.66	0.48	E	S	29.80	51.20	19.00	68.30	31.70	0.00	0.00	52.00
MZA	12.00	0.81	0.33	0.35	0.17	S	C	6.80	93.20	0.00	13.00	76.10	10.90	0.00	41.00

Sites: Doña Petra Canyon (CDP); Ecoterra (ECO); La Bufadora (BUF); Libramiento (LIB); Maneadero (MZA); Mirador (MIR); CETYS Hill (CET); Rancho Horsepower (RHP); Valle Dorado (VDO). Diversity measures: S—Species richness; H—Shannon–Wiener Index; E—Pielou’s evenness, D—Simpson’s index; Rao—functional diversity. OR—Compass orientation. Soil texture: S—sandy; R—rocky; C—clay. Vegetation: %S—shrub; %H—herbaceous; %B—bare ground.

3.3. Ecological Variables Influencing Species Abundance and Richness

Two CCA dimensions explained the variance in ant species abundance, indicating a strong linear relationship between two environmental variables (site orientation and soil type) and species abundances. The variation in species composition across sites is largely explained by northern exposures and rocky soils at one end of each axis and sandy soils with southerly exposures at the other (Figure 4). Nectivore, granivore, and harvester feeding guilds were positively associated with sandy soils and southern exposures. Generalists were found at all sites, but the highest abundances were recorded at sites with sandy soils, southern exposures, and herbaceous vegetation.

The CCA result was confirmed by a cluster analysis that revealed four groups of sites, (Figure 5; Table 2). Each group shared common physical and biological characteristics. The Rancho Horsepower (RHP) and Ecoterra (ECO) sites, characterized by high elevation, southern exposure, sandy soils, and high species richness, were clustered together. Another cluster represented sites with northern exposures and rocky or compact soils, including the Doña Petra Canyon (CDP), Mirador (MIR), La Bufadora (BUF), and Valle Dorado (VDO) sites. The Libramiento (LIB) and Maneadero (MZA) sites, at similar elevations with

comparable species richness, were grouped together. The CETYS Hill (CET), a westerly facing site with the lowest species richness, was separate from other groupings.

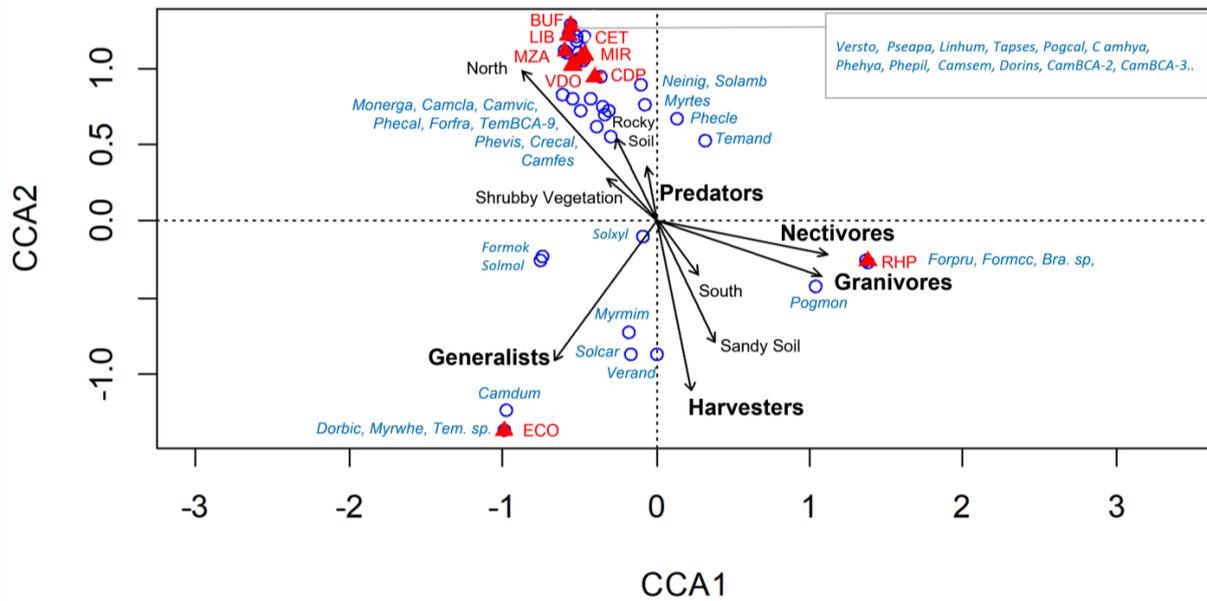


Figure 4. CCA biplot with constraining variables illustrating associations of ant species with biological and environmental gradients across the CSS sample sites. Feeding guilds are in bold. Arrows—physical and biological variables; open blue circles—ant species; solid red triangles—sampling sites, including Doña Petra Canyon (CDP); Ecoterra (ECO); La Bufadora (BUF); Libramiento (LIB); Maneadero (MZA); Mirador (MIR); CETYS Hill (CET); Rancho Horsepower (RHP); Valle Dorado (VDO). Species names are 6-letter taxon codes (first 3 letters of genus name plus first 3 letters of species name; see full species list in Table 1).

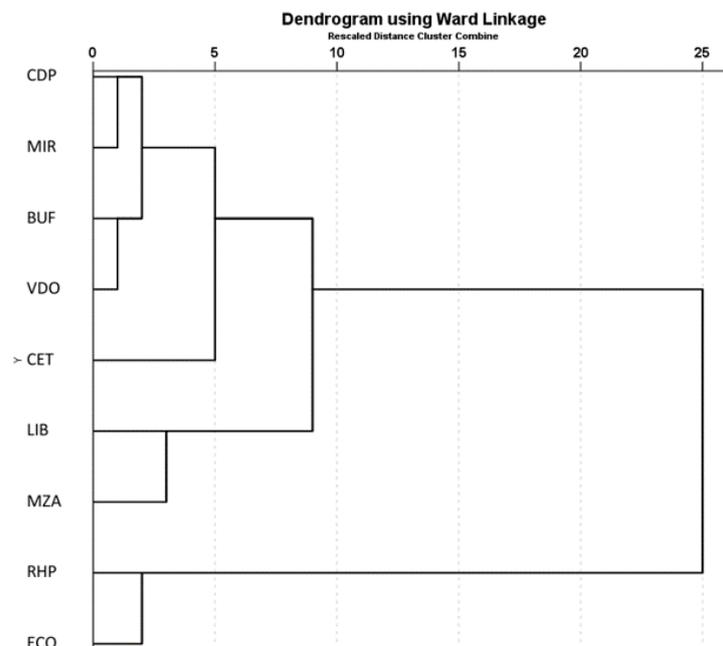


Figure 5. Diversity measures and environmental variables were used in a cluster analysis to evaluate patterns of similarity between CSS sampling sites. Doña Petra Canyon (CDP); Ecoterra (ECO); La Bufadora (BUF); Libramiento (LIB); Maneadero (MZA); Mirador (MIR); CETYS Hill (CET); Rancho Horsepower (RHP); Valle Dorado (VDO).

4. Discussion

With the exception of *Brachymyrmex* sp.1 and *Temnothorax* sp.1, yet to be identified, all of the species recorded in this study have been reported for the State of California (USA). This is not surprising given the geographic continuity of the Baja California Peninsula and that Ensenada is within the California Floristic Province (CFP). Thirty percent of the species observed in this study have distributions limited to the CFP. However, a higher proportion (43%) of the observed species have a much wider geographic distribution. This is likely due to Ensenada's location in the south of the CFP and its proximity to a desert transition zone. The taxa begin to change quickly, moving south from the bands of CSS near Ensenada (31.1° N) to El Rosario (30° N) in the southernmost region of the Mediterranean Climate Zone [46,47].

Johnson and Ward reported 176 species for the entire Baja Peninsula [32]. This study recorded 23% of those species, with the notable omission of any endemic species previously reported. Finding so many species in a relatively small area may be an artifact of the low number of intensive sampling studies completed on the peninsula. However, our observation also supports the assumption by Johnson and Ward that their list was incomplete, a conjecture further supported by our discovery of two previously unreported species for the peninsula (*Brachymyrmex* sp.1 and *Solenopsis carolinensis*).

4.1. Ecological Characteristics

We found significant relationships between soil type and abundance of ants and functional diversity, reinforcing previous work showing that soil strongly affects the composition of ant communities [48]. The species we observed with highest relative abundances, including *Forelius mccooki* (nectivore/generalist) and *Dorymyrmex bicolor* (generalist and abundant), were associated with loose sandy soil and more herbaceous vegetation. Seed dispersing species such as *Veromessor andrei* and *Pogonomyrmex montanus*, known to modify soil and vegetation structure and influence community structure [49,50], were also associated with loose soil structure.

One explanation consistent with our observation of decreasing species richness in compact and rocky soils is that nesting in open sites with loose soil structure is metabolically efficient in warm arid areas and helps regulate heat within the colony. This differs markedly from cold arid environments such as tundras, where ants construct nests under rocks (i.e., thermal shields); tropical forests, where ants clear gaps to facilitate heat exchange [50]; or temperate forests, where ants build large epigeous mounds to trap solar radiation [51]. Nesting in loose soils would also facilitate the growth of larger nests toward the soil interior.

Likewise, the compass orientation of the sites determines the effect of direct exposure to sunlight. In the Ensenada area, south-facing slopes indirectly receive higher humidity in the spring and summer due to strong winds (up to 35 km/h) that bring dense fogs from the northeast [52]. This helps to keep soil temperatures low. Meanwhile, the north and west slopes receive greater intensity from the sun, which increases surface temperatures and water evaporation from the soil. In keeping with the observed site physical characteristics, higher species richness was observed in the sites oriented to the south (22 species in RHP and 20 in ECO) and east (20 species in CDP).

Dauber et al. [43] found that variations in ecological variables similar to those measured in this study were unlikely to explain ant species richness unless the community structure was measured at an appropriate scale (e.g., the regional level; [40,53]), considering patches of vegetation of greater size and age. This suggests that environmental factors such as temperature, which we did not measure, must be included in any analysis of species richness. Other authors suggest that species richness is better explained at the landscape scale in which the analysis is carried out [54]. Considering the distribution of ant species along the coastal scrub area, it is likely that physical factors influencing species richness would be evident on a larger scale than presented here. A more robust analysis would have included a finer-scale measurement of factors known to directly impact ant

populations, such as food availability, microclimate measures of temperature and humidity, and interactions between populations that regulate access to available resources [50].

4.2. Feeding Guilds and Functional Diversity

Andersen [55] found that ant feeding guilds, or functional groups, are highly predictive bioindicators of ecosystem responses to environmental perturbation. Functional groups transcend taxonomic levels, allowing comparisons between communities with little species overlap [55]. In other words, the reliability of predictions about ecosystem health based on species data may be low. However, if predictions are made from cross-taxonomic data at the level of functional groups, they may be a more accurate reflection of patterns of species succession, rehabilitation, and reestablishment [56]. In this study, we examined species abundance by both feeding guild and ecological conditions at each sampling site. Sites with predominantly sandy soil supported more feeding guilds and an increased relative abundance of the rarest feeding guild recorded in our samples (harvesters). Compact or rocky soil types supported fewer feeding guilds and were dominated by generalist species.

Generalist ant species have a wide dietary range and use a variety of foraging behaviors, including scavenging, predation, and harvesting plant material. In undisturbed habitats, generalist ants are often abundant and diverse [57]. However, in disturbed or fragmented habitats, where specific food sources may be limited, specialist species can increase in number, boosting functional diversity in edge areas [58]. For example, *F. mccooki*, a dominant nectar-feeding species that can limit resources to other species [59], can be a key species for community structure. Indeed, in this study, the site supporting the highest species richness (RHP) had the highest abundance of *F. mccooki*. The only other site where *F. mccooki* was recorded (CDP) hosted the highest functional diversity of all sites.

Two ant species, *C. californica* (generalist/nectivore) and *P. vistana* (predator), were numerically significant across all nine sampled sites. These pervasive species are agile, aggressive, recruit extensively, interact interspecifically, and tend to form groups with other species of similar behavior, a pattern reflected in Figure 4. As a result, they are able to displace less aggressive species that may occur in small numbers [60], decreasing species richness and functional diversity at the sites in which they were most abundant.

It is surprising that only one invasive ant species, *Linepithema humile*, was identified in our samples despite prior observations of other non-native species in the Ensenada urban area (e.g., *Paratrechina longicornis* and *Monomorium pharaonic* [32]). The presence of *L. humile* is likely associated with the unique ecology of peri-urban areas; the species prefers urbanized edges and areas dominated by introduced vegetation [61]. That *L. humile* was found in only one trap at one site may indicate its recent arrival in the area and that it is likely in the early stages of expansion. This species is known to displace seed disperser ant species, which subsequently alters plant recruitment and the composition of the local plant community [62]. *Linepithema humile* may also displace other arthropod species and can efficiently exploit the resources of relatively small areas [63]. This is problematic as the native flora and fauna of Ensenada's peri-urban areas depend on larger areas and better-conserved habitats [64]. The potential impact of *L. humile* and other introduced species warrants better population monitoring in this region and detailed documentation of geographic expansion in the coastal sage scrub.

Increased functional diversity within communities promotes ecosystem productivity, stability, and resilience and perhaps ultimately reduces invasion by non-native species. Our analysis suggests that peri-urban sites with southerly exposures, sandy soil, and vegetation predominated by herbaceous plants (grasses, forbs, etc.) at higher elevations supported the highest functional diversity among the CSS ant communities. Prior work in other Mediterranean Climate Zones has shown a similar pattern with respect to sandy soils and vegetative cover supporting increased ant species richness [65]. Preserving areas with similar characteristics should be a priority to protect native ant species diversity on the Baja Peninsula.

Our findings also underscore the significance of obtaining detailed biological data with spatially specific information for the unique coastal scrub in Ensenada's peri-urban area. This ecosystem's high species richness and diverse flora highlight its fragile nature. Detailed studies in CSS areas facing constant disturbance and destruction are therefore important. Since data collection in 2009, the Doña Petra Canyon sampling site has been lost to urban expansion, and another area near the Ecoterra site (La Encantada) has burned. Data such as those presented in this study record historical information on species that previously inhabited these sites and can be used to document the progression or colonization mechanisms in areas exposed to disturbance.

5. Conclusions

These presented results fill a gap in the existing literature on ant species of the Baja Peninsula of Mexico and highlight the fact that the inevitable dispersal of invasive species, such as the Argentine ant, *Linepithema humile*, will present challenges for the management of coastal sage scrub areas. Our work emphasizes that the characterization of peri-urban sites and their relationship to the diversity of ant species is essential and should be considered in future proposals for coastal sage scrub habitat protection and restoration.

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