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The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities

Kevin M. Clarke · Brian L. Fisher · Gretchen LeBuhn

Abstract As rapid urbanization continues, existing natural areas within urban zones will play a critical role in safeguarding remaining biodiversity. Ants are an integral part of almost every terrestrial ecosystem, including urban environments, and understanding which environmental characteristics influence their persistence is critical. In this study, 24 protected natural areas within urban parks including mosaic, scrub, herbaceous and forest habitats were surveyed for ants with 563 pitfall traps. The data provide insights into the distribution and abundance of ant fauna in San Francisco natural areas, as well as which characteristics of parks have the most influence on ant community composition. A total of 2,068 ant individuals representing 15 species were collected. A regression analysis revealed that urban forests reduced ant richness and abundance and that there was little or no impact of the Argentine ant on native ants. Natural area size and shape were not important in explaining variations in overall ant species richness and abundance, with many smaller natural areas harboring ant populations that are just as diverse and robust as larger areas.

Keywords Urbanization · Natural areas · Argentine ant · San Francisco · Forest · Conservation

Introduction

The process of urbanization has led to a pervasive transformation of natural ecosystems. This process not only consumes natural habitats, but also fragments, degrades, and isolates remaining natural areas, which are then entrenched in a matrix of anthropocentric land uses. This transformation has profound and often detrimental effects on the remaining native

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K. M. Clarke · G. LeBuhn (✉)
Department of Biology, San Francisco State University, 1600 Holloway Avenue,
San Francisco, CA 94132, USA
e-mail: lebuhn@sfsu.edu

B. L. Fisher
Department of Entomology, California Academy of Sciences, San Francisco, CA 94118, USA

biota (Suarez et al. 1998; Gibb and Hochuli 2002) and the process of urbanization shows no signs of slowing globally. By 2008, for the first time ever, more than half of the world's human population will live in urban areas. This trend is projected to swell to almost two-thirds of the world's population by the year 2025 (United Nations 2004). With urbanization increasing in both size and scope, in addition to growing concerns about the magnitude of global biodiversity loss (Gaston 1996), natural areas within the urban envelope will play a growing and critical role in species preservation (Adams 2005; McFrederick and LeBuhn 2006). Previous studies have recognized that urban landscapes may present considerable opportunities to conserve existing biodiversity that might otherwise be lost (Frankie and Ehler 1978; Dickman 1987; Suarez et al. 1998; Bolger et al. 2000; Connor et al. 2003; McFrederick and LeBuhn 2006). Within cities, urban parks provide a significant opportunity to retain some of this biodiversity. Understanding the characteristics of areas that enhance biodiversity is critical in order to preserve and manage them effectively (Niemela 1999; McIntyre et al. 2001).

In order to survive in urban parks, species must adapt to a wide array of biotic and abiotic factors related to urbanization. The most evident impact of urbanization is habitat loss due to fragmentation. A decrease in habitat area can reduce population sizes (Bolger et al. 2000) and cause local extinctions (Soulé 1987; Drayton and Primack 1996; Mangel and Tier 1994). Furthermore, reduced gene flow attributed to small, isolated populations can lead to inbreeding and reduced fitness in urban populations (Hitchings and Beebee 1998). Fragmentation also increases edge effects, which change the microclimate, physical properties and livable area available to some species (Saunders et al. 1991). Edge effects also facilitate the invasion of exotic species (Suarez et al. 1998) and can increase predation by domestic animals (Crooks and Soulé 1999). Urban species must also adapt to higher urban temperatures compared to rural areas (Baur and Baur 1993; Angilletta et al. 2007) and urban parks often have increased levels of pollution and soil compaction (Pyle et al. 1981; Jim 1998). Yet even these degraded and challenged ecosystems can yield sizable numbers of important species, especially in areas of high native diversity and endemism.

San Francisco, California is the second most densely populated city (with populations over 200,000) in the USA (US Census Bureau 2000) and is located within a biodiversity hotspot harboring a number of rare and endemic species (Connor et al. 2003; EIP Associates 2005). Urbanization has already taken a heavy toll on the biodiversity of San Francisco. Three butterfly extinctions, including the first recorded in the USA, have been recorded within city limits and are attributed to habitat loss due to development (Tilden 1956; Connor et al. 2003). Hafernik and Reinhard (1995) estimated that 43% of the city's butterfly species have been lost due to habitat loss. Furthermore, several bumblebees were found to be locally extinct in urban parks (McFrederick and LeBuhn, 2006) and the endangered forktail damselfly (*Ishnura gemina*) has gone extinct in a large protected park due to overgrowth of its habitat (Connor et al. 2003). These species disappearances, many of which occurred in and around protected areas, demonstrates the importance of identifying habitat characteristics that encourage the persistence of biodiversity. Unfortunately, information for land managers in urban areas is lacking for most taxa (Connor et al. 2003). This is particularly true for invertebrates such as ants (Suarez et al. 1998; Yamaguchi 2005; Thompson and McLachlan 2007).

Ants play an integral role in almost every ecosystem they inhabit (Hölldobler and Wilson 1990), including urban environments (Thompson and McLachlan 2007). Ants move and enrich soil, distribute plant seeds, are an important food for many animals, and can act as chief predators of small invertebrates (Beattie 1985; Montanucci 1989; Hölldobler and Wilson 1990; Folgarait 1998; Thompson and McLachlan 2007). Ants may also be excellent indicators of land management practices and restoration efforts because they are sensitive to habitat variation, respond quickly to changes in habitat quality and are easy to collect and identify (Andersen et al. 2002; Underwood and Fisher 2006). California has a rich diversity of ants (~281 species) and, due to its climatic and geographic features, has a high level of endemism (13.9%) compared to adjacent regions (Ward 2005).

The effects of urbanization on ants and the characteristics of urban natural areas that enhance their biodiversity are still unclear. However, a few studies are starting to expose urbanization's impact on ants and reveal characteristics that are key to ant persistence (Suarez et al. 1998; Lopez-Moreno et al. 2003; Lessard and Buddle 2005; Yamaguchi 2005; Pacheco and Vasconcelos 2007; Thompson and McLachlan 2007). Among these is the size of remaining natural fragments. In general, larger natural fragments support a greater number of species while smaller fragments reduce population sizes and species richness (Suarez et al. 1998; Bolger et al. 2000; Yamaguchi 2005). However, a few studies have shown no difference in species richness between large and small fragments and, in some cases, smaller fragments may exhibit greater species richness (Gibb and Hochuli 2002; Dauber et al. 2006). Another feature of fragmentation is that it increases edge effects, which can promote the establishment of invasive species and reduce native ant populations (Suarez et al. 1998).

One of the most successful invasive species in urban environments, the Argentine ant (*Linepithema humile*; Knight and Rust 1990), has expanded its range to San Francisco. Since the Argentine ant was first recorded in California in 1907 (Newell and Barber 1913), urbanization has hastened its proliferation (Suarez et al. 2001). This invasive pest causes a number of negative impacts on native species. Many studies have found that the Argentine ant reduces native ant diversity (Ward 1987; Human and Gordon 1996; Human and Gordon 1997; Suarez et al. 1998) and causes a number of deleterious secondary effects. For example, Bond and Slingsby (1984) found a disruption of ant-plant mutualisms when Argentine ants displace native ants that are seed dispersers. Sanders et al. (2001) found that Argentine ants displace native ants that tend lycaenid butterfly larvae, which could potentially impact the endangered mission blue butterfly (*Icaricia icarioides missionensis*) that inhabits many San Francisco parks.

This study aims to provide baseline data on ant species diversity and community composition and identify natural area characteristics important for San Francisco's ant communities. Specifically, it seeks to determine (1) the distribution and abundance of ant fauna in San Francisco natural areas; (2) which characteristics of natural areas influence the observed patterns of distribution and abundance; (3) whether species richness and community composition differences exist in the city's four dominant natural habitats; and (4) whether the Argentine Ant has an impact on native ants.

Methods

Study sites

San Francisco has a coastal Mediterranean climate with dry moderate summers and wet mild winters (Ahrens 1994). The dry season typically extends from May to October and the wet season from November to April. On average, San Francisco receives 95% of its annual rainfall from late October through March (Null 1992). The combined effects of regional climate trends, San Francisco's hilly topography and maritime surroundings produce a number of extremely varied microclimates within city limits.

We sampled 24 urban parks in San Francisco, California (37°46′0″ N 122°26′0″ W) that contain sites designated as Significant Natural Areas (hereafter called "natural areas"; Fig. 1). Natural areas are defined as having remnant fragments of the historic Franciscan Landscape (Forman 1995) that have persisted largely unchanged by human activity (EIP Associates 2005). These areas contain a myriad of plant and animal communities that differ dramatically from one another and support many sensitive plant and animal species (Connor et al. 2003; EIP Associates 2005). Habitats include coastal scrub, dunes, annual and perennial grasses, chaparral, riparian wetlands, lakes, rock outcrops, and native patches of coastal live oak and laurel trees. These natural areas, however, should not be considered pristine, as many are dominated by non-native plant species. For example, non-native eucalyptus covers large portions of many of these areas. San Francisco residents and visitors access these natural areas for passive recreational purposes such as hiking, nature watching, and dog walking. There are 30 urban parks with natural areas in the city, which range in size from 0.12 ha to over 66 ha. We selected 24 parks for sampling. Six parks were eliminated from the study due to the potential for significant pitfall disturbance or concern for pet safety. Also, The Presidio, a large area in the city with areas of natural area, was not sampled because it is not managed by the San Francisco Park and Recreation Department. Selected parks ranged in size from 0.12 acres to 24.28 ha (Appendix 1).

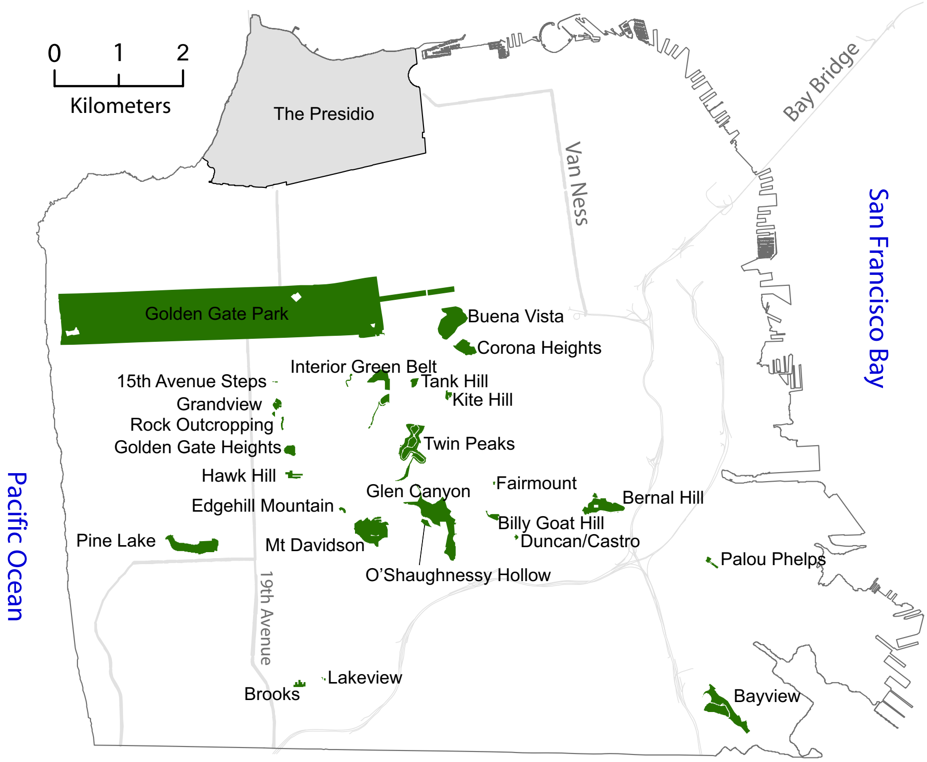

Fig. 1 Map of sampled parks in San Francisco, CA

Study organisms

According to a survey of museum records, 21 species of ants have been collected in the city of San Francisco: *Aphaenogaster occidentalis*, *Camponotus laevigatus*, *Camponotus vicinus*, *Crematogaster coarctata*, *Formica francoeuri*, *Formica fusca*, *Formica lasioides*, *Formica moki*, *Formica subpolita*, *Formica transmontanis*, *Hypoponera opacior*, *Lasius pallitarsis*, *Linepithema humile*, *Monomorium ergatogyna*, *Pogonomyrmex subdentatus*, *Prenolepis imparis*, *Stenamma diecki*, *Tapinoma sessile*, *Technomyrmex difficilis*, *Temnothorax andrei*, and *Tetramorium caespitum* (Fisher et al. 2007). All but *Linepithema humile*, *Technomyrmex difficilis, and Tetramorium caespitum* are considered native (Ward 2005).

Sampling method—ant abundance and species richness

To estimate ant abundance and species richness, we sampled parks using pitfall traps and general collecting methods. Pitfall traps are considered an effective way to obtain a representative sample of ant communities (Andersen 1995). Each pitfall trap consisted of a 28 mm-wide (internal diameter of mouth) 50 ml Fisher-brand test tube filled halfway with a 50:50 mixture of water and non-toxic antifreeze. Because of the large number of dogs and other mammals that use city parks, Sierra-brand antifreeze (Safe Brands, Omaha, Nebraska, USA) was used because it is non-toxic and doubles as an excellent insect preservative. Traps were buried with minimal disturbance with the lip of the pitfall trap flush with the ground surface. In each park, five pitfall traps were placed in each hectare of natural area, with two pitfall traps considered the minimum for fragments smaller than a hectare. Each point was sampled once from August to September 2006, with each of the 545 pitfall traps set in the 24 natural areas left open for a 48-h sampling period.

To assign pitfall points in each park, we used a Geographical Information System (GIS) random sampling program (Beyer 2004), which placed between 2 to 117 pitfall traps in each park (Appendix 1). The order in which parks were sampled was randomized and points in parks were located with a GPS unit and printed GIS maps.

In addition to pitfall sampling, extensive visual surveys were conducted in each park to ensure that all ground-foraging ants were detected within the park. Surveys consisted of walking between each pitfall point during pitfall trap collection, overturning objects, and aspirating samples of all ants observed. Specimens collected in visual surveys were only included in species richness results and not abundance data. *Solenopsis* and *Stennama* species were excluded from analysis because they are not effectively sampled with pitfall traps (Suarez et al. 1998). These species, however, were included in species distribution results (Tables 1 and 2).

Following trapping, pitfall traps were capped and removed to the laboratory for processing. Ant specimens collected were washed and stored in 95% ethanol until identification. Worker ants in each trap were counted and identified to species. Brian Fisher of the California Academy of Sciences and Phil Ward of UC Davis verified most species identifications. All specimens for this study are housed in the Department of Entomology at the California Academy of Sciences, San Francisco, CA except for a voucher set at San Francisco State University.

Sampling method—park characteristics

We measured park characteristics that are known to influence the distribution and abundance of ants (Appendix 1). Variables included park size, park shape (edge effect),

Table 1 All species found in San Francisco parks (parks 1–12)

Species	Endemis Score	Brooks Park	Twin Peaks	Bayview	Bernal Hill	Lakeview Mini Park	Golden Gate Park	Palou Phelps	Golden Gate Heights	Hawk Hill	Rock Outcrop	Grandview Park	Billy Goat Hill
Linepithema humile	0.04	1	1	1	1	1	1	1	1	1	1	1	1
Temnothorax andrei	0.29	1	1	1	1	1				1	1	1	1
Monomorium ergatogyna	0.42	1	1	1	1	1		1		1			1
Tapinoma sessile	0.50	1	1		1	1				1	1	1	1
Aphaenogaster occidentalis	0.71	1	1		1	1							1
Formica lasioides	0.79		1						1	1	1	1	
Prenolepis impairs	0.83		1	1				1					
Formica fusca	0.92	1				1							
Pheidole californica	0.92			1									
Camponotus vicinus	0.96		1										
Formica subpolita	0.96		1										
Temnothorax nevadensis	0.96				1								
Tetramorium caespitum	0.96	1											
Solenopsis molesta[a]			1	1	1								
Stennema diecki[a]							1						
Park species total		7	9	5	6	6	1	3	2	5	4	4	5
Park endemism score		0.55	0.50	0.50	0.49	0.48	0.48	0.43	0.42	0.41	0.41	0.41	0.39

Top table lists parks 1–12. Table includes endemism score (high scores indicate more unique species) for each species as well as presence/absence per park. Species are sorted from most common to least common and parks are sorted by endemism scores from high to low

[a] Detected but not included in analysis (see methods)

Table 2 All species found in San Francisco parks (parks 12–24)

Species	Mt. Davidson	O'shaughnessy	Kite Hill	Glen Canyon	Tank Hill	Pine Lake	Corona Heights	Fairmount Park	Edgehill Mountain	Buena Vista Park	15th Avenue Steps	Interior Green Belt	Ubiquity
Linepithema humile	1	1	1	1	1	1	1	1	1	1	1		23
Temnothorax andrei	1	1	1	1	1	1		1	1				17
Monomorium ergatogyna	1		1	1	1	1	1						14
Tapinoma sessile	1			1	1	1							12
Aphaenogaster occidentalis	1		1										7
Formica lasioides													5
Prenolepis imparis		1											4
Formica fusca													2
Pheidole californica				1									2
Camponotus vicinus													1
Formica subpolita													1
Temnothorax nevadensis													1
Tetramorium caespitum													1
Solenopsis molesta[a]	1			1									
Stennema diecki[a]													
Park species total	5	3	4	5	4	4	2	2	2	1	1	0	
Park endemism score	0.39	0.39	0.36	0.33	0.31	0.25	0.23	0.17	0.17	0.04	0.04	0.00	

The bottom table lists parks 13–24. Table includes endemism score (high scores indicate more unique species) for each species as well as presence/absence per park. Species are sorted from most common to least common and parks are sorted by endemism scores from high to low

[a] Detected but not included in analysis (see methods)

soil moisture, the abundance of the invasive Argentine ant, percentage of four dominant vegetation types and habitat heterogeneity for each park. Park size was derived from existing data (EIP Associates 2005). Park shape was quantified using a complex perimeter/area ratio (Patton 1975) called an irregularity index (Suarez et al. 1998). It was calculated for each fragment using GIS maps and dividing the amount of edge around the park by the circumference of a circle (the geometric shape with the smallest amount of edge per area) of the same area as the fragment. As fragment shape becomes more irregular, the index increases without limit above a value of 1 and represents the amount of edge specific to a selected fragment relative to the fragment size. Soil moisture for each park was determined by taking a soil core for each point at the completion of the 48-h sampling period. A bulb planter was used to take a soil core within a one meter radius of each pitfall, which was then placed in a paper lunch bag and brought to the laboratory to have the wet weight measured. The samples were then dried at 90°C for 48 h and re-weighed. Soil moisture was calculated by taking the difference between dry and wet weight and dividing by the wet weight. Soil samples for each park were pooled together and divided by the total number of samples to determine an average for the park. The percentage of the four dominant vegetation types (forest, grassland, scrub and mosaic—areas of mixed vegetation, e.g. 'grassland-scrub') were estimated using available data from the San Francisco Recreation and Parks Department (EIP Associates 2005). Habitat heterogeneity, which was based on the number of vegetation types in each natural area, was derived data provided by the same agency (EIP Associates 2005).

Data analysis

Species richness for each park was determined by total number of species pooled from pitfall sampling and visual surveys. The total number of workers divided by number of pitfall traps quantified species abundance for each park. Because pitfall sampling may bias ant abundance due to the chance proximity of a pitfall trap to a nest, the effect of a substrate on forager activity, and variable species response to pitfall traps (Bestelmeyer and Wiens 2001), all ant abundances were log-transformed [$\log(n+1)$] at the trap level to normalize data.

To model the park characteristics which best explain differences in ant species richness, native species richness, ant abundance, Argentine ant abundance and endemism between parks, we analyzed the data using ordinary least squares regression. Response variables were transformed when necessary to meet the assumptions of regression (Zar 1999). Prior to regression analysis, we tested for collinearity and constructed a correlation matrix to examine possible relationships among park characteristics. Two sets of models were built using forward regression (p to enter the model <0.05) with SPSS (2001, v. 11.01), one with number of pitfall traps for each park as a covariate and one without a covariate. Since the results were consistent, we are only presenting results with a covariate. To quantify endemism for each park, we created an endemism index for each ant species based on the number of parks in which each species was found. We divided the number of parks a species occurred in by the total number of parks and subtracted this number from one (Tables 1 and 2). The index ranged from 0.93 (unique) to 0 (ubiquitous; note that the highest index does not equal 1, because there must be at least one park per species and a score of one would indicate zero parks per species). We calculated an average endemism for each park (summed all scores averaged over number of ants) and used this metric in building the models.

Five different regression models were built. The dependent variables were species richness, native species richness, ant abundance, Argentine ant abundance, and park endemism. Potential explanatory variables were park size, park shape, soil moisture, Argentine ant abundance (not used in model with abundance of Argentine Ant as dependent), percentage of the four dominant vegetation types and habitat heterogeneity. We examined the pattern of the residuals for each regression model and found no evidence to suggest that linear regression was not the appropriate model for these data.

To compare the four dominant vegetation types, pitfall traps were pooled together in each vegetation type. Dominant vegetation types were forest (dominated by *Eucalyptus globulus*), herbaceous (dominated by annual grassland, mainly *Avena* sp.), scrub (dominated by *Baccharis pilularis* and *Genista monspessulana*) and mosaic (dominated by *Avena* sp./*Baccharis pilularis* mosaic). To assess community composition similarity among vegetation types, a pairwise species composition similarity was calculated using the Marczewski–Steinhaus (M–S) distance index (Colwell and Coddington, 1994):

$$\mathrm{MS} = \frac{w}{a + b - w}$$

where a=number of ant species of one vegetation type, b=number of ant species of the second vegetation type, and w=number of ant species common to both vegetation types.

Results

Community structure

A total of 2,068 ants were captured between August and September 2006 belonging to 11 genera and 15 species. Four of these species had not been previously recorded in San Francisco County (*Pheidole californica*, *Solenopsis molesta*, *Stenamma* sp. 1 cf. *punctatoventre* and *Temnothorax nevadensis*), though are known from surrounding counties. The species detected in this study comprise 60% of the 25 species (including four new species detected in this study) that have historically been recorded in San Francisco. Species richness in each park ranged from zero in a park dominated by eucalyptus (Interior Green Belt, Tables 1 and 2) to nine species found in a park dominated by patches of grassland and scrub (Twin Peaks, Tables 1 and 2). Average ant abundance between parks ranged from 0 (Interior Green Belt) to 33.5 (Brooks Park) individuals per trap. The most abundant species, accounting for 29% of individuals collected, was *Monomorium ergatogyna*, a small (about 2 mm long), common, ground-nesting species. This species was found in 14 parks. The second most abundant species, accounting for 26% of individuals collected, was the Argentine ant. This species was the most commonly encountered species, appearing in every park but one. There were also two uncommon species collected: one *Stenamma* sp. 1 cf. *punctatoventre* in Golden Gate Park and two *Temnothorax nevadensis* in Bernal Hill park. Endemism, which is a measure of park uniqueness (a higher value represents a more unique fauna), ranged from 0 in the Interior Green Belt to 0.55 in Brooks Park (Tables 1 and 2), a smaller park dominated by grassland.

Influence of park characteristics

The model examining species richness revealed that soil moisture and percent of natural area that is forest explained 58% of the variation in species richness between parks ($F_{3,\,20}$= 11.525, p<0.0005, adjusted R^2=0.579, Table 3). Soil moisture was positively related to species richness and percent of natural area that is forest was negatively related.

Table 3 Regression model variables and coefficients with adjusted R^2 values in bold and positive or negative correlation indicated

Dependent variable	Independent variables	Correlations (respectively)	Adjusted R^2 for whole model
Species richness	Percent forest and soil moisture	Negative and positive	0.58
Native species	Percent forest and soil moisture	Negative and positive	0.62
Ant abundance	Percent forest	Negative	0.47
Argentine ant abundance	No variable fit model		
Endemism index	Percent forest	Negative	0.52

The model testing ant abundance as the dependent revealed the percent of park that is forest was significantly negatively correlated and accounted for 47% of the variation in ant abundance among parks ($F_{2,\ 19}=10.263$, $p=0.001$, adjusted $R^2=0.469$, Table 3).

The model investigating native species richness as the dependent revealed soil moisture and percent of park that is forest explained 62% of the variation in native species richness between parks ($F_{3,\ 20}=13.418$, $p<0.0005$, adjusted $R^2=0.618$, Table 3). Soil moisture was positively correlated with native species richness and percent of natural area that is forest was negatively correlated.

The model testing mean park endemism as the dependent revealed that the percent of forested area was significantly negatively correlated and accounted for 52% of the variation in mean endemism among parks ($F_{2,\ 21}=13.469$, $p<0.0005$, $R^2=0.520$, Table 3).

Impact of the Argentine ant on native ant species

No model explained the variation in Argentine ant abundance. Argentine ants were detected in 23 of the 24 parks, indicating it is ubiquitous in San Francisco parks. However, in 12 of the parks, Argentine ants were not detected in pitfall traps. Instead, their presence was confirmed in visual surveys. In these parks, Argentine ants were observed only around park perimeters (personal observation). This suggests Argentine ants are limited to park perimeters and are not abundant in park interiors. Of the pitfall traps that contained Argentine ants, over 75% contained fewer than five Argentine ants, suggesting these parks also had relatively low abundances in their interiors. Overall, Argentine ants were found in only 18% ($n=100$ traps) of total traps with a mean abundance of 5.5 individuals per trap. Of the traps with Argentine ants, 65% did not contain any other ant species. The traps that did contain other species included only *Monomorium ergatongyna*, *Prenolepis imparis*, *Temnothorax andrei* and *Tapinoma sessile*.

Ant community in four dominant vegetation types

Ant species richness was noticeably lower in forest habitats (Table 4). The five species detected within forests were also found in the three other habitats. Scrub and mosaic have the most similar ant communities, sharing eight species. The Marczewski–Steinhaus (M–S) Complementarity Index, which is a measure of beta diversity (Magurran 2004), shows that species turnover is greatest between forest and herbaceous vegetation habitats (Table 5). The difference in ant communities between forest and the three other habitats examined may be explained, in part, by soil moisture. The forest vegetation had an average soil moisture of 10.3%, compared to just 2.8% in herbaceous, 3.4% in mosaic, and 4.3% in scrub (Fig. 2). Within forest vegetation types, traps ($n=19$) that contained ants had a mean

Table 4 List of ant species found in four park dominant vegetation types

	Forest	Mosaic	Scrub	Herbaceous
Linepithema humile	*	*	*	*
Monomorium ergatogyna	*	*	*	*
Temnothorax andrei	*	*	*	*
Tapinoma sessile	*	*	*	*
Prenolepis impairs	*	*	*	*
Aphaenogaster occidentalis		*	*	*
Temnothorax nevadensis				*
Camponotus vicinus		*	*	*
Pheidole californica			*	*
Formica lasioides		*	*	*
Formica fusca				*
Formica subpolita		*	*	
Tetramorium caespitum				*
Total species	5	9	10	12

soil moisture of 4.5%. This was very different than traps in forests without ants, which had a mean soil moisture of 11.5% ($n=171$) suggesting soil moisture plays a role the distribution of ants in the urban forest. Herbaceous habitat had the richest ant community and the most unique species.

Discussion

Influence of park characteristics

This study indicates that both the amount of forest vegetation and soil moisture are important characteristics in explaining the distribution of ants in San Francisco parks. The percent of park that is forest was a significant variable in four of the five models tested, suggesting this vegetation type has a strong negative impact on the ant community. Urban forests embedded in parks supported very few ants and may limit the habitable areas to remaining non-forested habitat. The most dramatic example of this was on Mount Davidson, which contains 75% closed canopy eucalyptus forest and 25% scrub and mosaic vegetation. The larger forested area did not support a single ant while the smaller scrub and mosaic areas supported five species and 4.04 ants per trap. Thompson and McLachlan (2007) reported a similar effect in Canada and found a simplified ant community in urban compared to suburban and rural forests. In California, previous investigations of urban ants

Table 5 The Marczewski–Steinhaus (M–S) complementarity measure between four vegetation types in San Francisco parks

	Forest	Herbaceous	Mosaic	Scrub
Forest	–	0.58 (5)	0.44 (5)	0.50 (5)
Herbaceous	–	–	0.36 (7)	0.33 (8)
Mosaic	–	–	–	0.11 (8)

Higher values represent greater distinctness with the number of species shared between vegetation types presented in parentheses

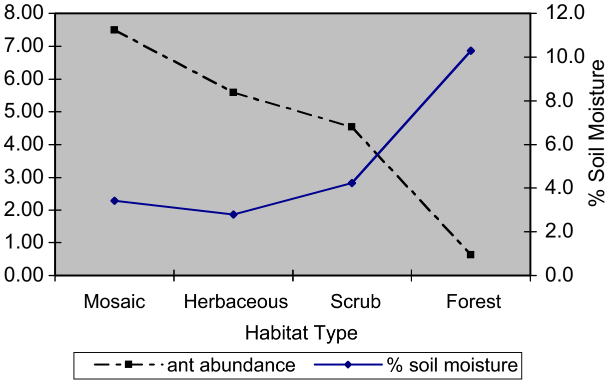

Fig. 2 Relationship between ant abundance and soil moisture in four habitat types

have focused on scrub, grassland and riparian habitats (Human and Gordon 1996; Suarez et al. 1998; Bolger et al. 2000; Holway and Suarez 2006). This is the first study to document the negative effect of urban forests in California.

Urban forests are structurally different than natural forests. Besides being smaller, fragmented and more isolated than non-urban forests, urban forests also show increased canopy cover (Dreistadt et al. 1990), greater disturbances due to human traffic and pollution, and differences in leaf litter accumulation (Thompson and McLachlan 2007). These changes can lead to lower plant and animal species richness (McIntyre et al. 2001; Moffatt et al. 2004) and a greater proportion of exotic plant and animal species (Dreistadt et al. 1990; Poland and McCullough 2006) compared to non-urban forests. In San Francisco, trees were not a conspicuous part of the historic landscape, and a majority of the trees in San Francisco today are not native to the area. The ants currently found in San Francisco (and based on historic collections) suggest that the majority of ants were adapted to open coastal prairie, grassland, or sandy (dune) habitats (Brian Fisher, pers. comm.). The alteration of biotic and abiotic characteristics of the city's natural areas by forests may help explain these impacts on ant communities.

Microclimatic conditions are also important in determining ant distributions (Perfecto and Vandermeer 1996). Studies have shown that increases in soil moisture, canopy cover, and habitat complexity are all associated with decreases in ant diversity and composition (Wang et al. 2001; Gotelli and Ellison 2002; Lassau and Hochuli 2004). A combination of high soil moisture, dense canopy cover, and dense understory (habitat complexity) may help explain the lack of ground-foraging ants in urban forests.

Urban forests in this study had increased average soil moisture compared to the three other major vegetation types (see Fig. 2). Even though soil moisture is positively correlated to overall species richness in parks (Table 3), very high levels of soil moisture may be unsuitable for ants in San Francisco because ant broods cannot grow in cold and wet environments. Prior studies have found increased soil moisture to be associated with lower nest densities in urban forests (Thompson and McLachlan 2007) and decreased ant abundance and diversity in North American forests (Wang et al. 2001). All ant species in San Francisco (besides the Argentine ant, which typically nests in leaf litter), are soil nesters, suggesting that increases in soil moisture have a direct impact on nest architecture, brood rearing and/or the incidence of harmful fungal infections at nest sites (Clark and Prusso 1986; Hölldobler and Wilson 1990). Within forest types examined, eucalyptus forests contained significantly more soil moisture than other forest types and also had lower ant richness and abundance. The increased moisture in eucalyptus is due to the fact that summer fog tends to condense on eucalyptus leaves and branches and drip down to the soil below. Such fog drip can add as much as 42 cm of water to eucalyptus forest soil during a single summer (Azevedo and Morgan 1974). Eucalyptus leaves also produce high concentrations of aromatic oils with allelopathic effects. As ants can be sensitive to soil properties (Johnson 1992; Fisher 1997), these effects may further inhibit the nesting habits of local ants.

Argentine ants were also absent or found in low abundances in urban forests. This finding is surprising, especially because the species is a ubiquitous urban pest and several studies in similar Mediterranean-type climates indicate this species prefers mesic over xeric sites (Suarez et al. 1998; Holway and Suarez 2006). In this study, Argentine ant abundance was not correlated with increased soil moisture (r=0.075) and no Argentine ants were found in traps (n=63) with soil moisture of 10% or greater. Wet environments with high levels of rain may not permit these ants to forage adequately (Vega and Rust 2001). Climatic differences may help explain discrepancies between this study and others showing that Argentine ants prefer moist conditions (Holway et al. 2002; Holway and Suarez 2006). For example, San Diego (Holway et al. 2002; Holway and Suarez 2006) has an average rainfall of ~250 mm, approximately half the average rainfall of San Francisco. Additionally, in San Francisco the dry season experiences a summer fog that may help maintain Argentine ant presence in drier areas.

The dense understory common in many of San Francisco's urban forests may also contribute to the scarcity of ants in this habitat. Urban forests in San Francisco are often carpeted with a dense, homogeneous, invasive understory of either Cape ivy (*Delairea odorata*), English ivy (*Hedra helix*) or Himalayan blackberry (*Rubus discolor*) (EIP Associates 2005). In San Francisco forests with a dense understory, no ants were detected, compared with a few ants found in urban forests with little or no understory (personal observation). Nor were ants detected outside of urban forests with similarly dense vegetation (i.e: iceplant—*Carpobrotus edulis*). A previous study found ant species richness to be negatively correlated with ground herb cover in a eucalypt-dominated habitat in Australia (Lassau and Hochuli 2004). Way et al. (1997) reports a similar finding with the Argentine ant, which dislikes dense vegetation. However, this study's result may be biased by the sampling method because pitfall traps are known to catch fewer insects in dense vegetation (Melbourne 1999). Nevertheless, ants were neither found in dense vegetation nor the forest understory during visual surveys supporting pitfall data.

Although temperature was not explicitly examined in this study, it may also play a role in determining the observed distributions. Ants are primarily thermophilic and Andersen (1995) has suggested that low temperature is the principal stress affecting ant community structure, to the point of limiting taxa diversity. Urban forests are distinctly cooler than other urban areas (Yilmaz et al. 2007), mainly due to the shade provided by the forest canopy. In San Francisco, shade from the tree canopy compounded by coastal fog during the summer can reduce forest temperatures by as much as 15°(F) in some areas of the city during the day (Gilliam 1962). The lack of solar radiation due to the thick forest canopy and extreme temperature changes may create an environment too stressful to support ants in urban forests. Add to this the collective effects of increased soil moisture, and a dense understory, and the result may be a microenvironment unsuitable for urban ants. Temperature may also play a role in explaining the distribution of ant communities in the other habitats examined in this study. In San Francisco's cool Mediterranean climate, vegetation types that allow more solar radiation to penetrate may be more ideal for thermophilic ants. Across all parks, the herbaceous vegetation, which is dominated by perennial and annual grasslands and characterized by low complexity, supported the most species (see Table 5). However, there were no clear differences in species composition between the mosaic, scrub, and herbaceous habitats (see Table 5).

Area is often a predictor of the number of species supported on an island or fragment (MacArthur and Wilson 1967), and is therefore a factor often considered in reserve design. However, park size did not correspond to any of the models in this study, suggesting size does not explain differences in richness and abundances of ants in San Francisco. This analysis holds true whether or not the number of pitfall traps was included as a covariate. We found that even the smallest park in San Francisco, Lakeview Mini park, which is just 0.16 ha, supports a rich ant fauna (6 species). Suarez et al.(1998) and Yamaguchi (2005), however, found different results in their urban ant studies, and report that larger parks support more species. Lastly, the number of habitats within a park fragment did not correspond to any regression models either. This may be because a majority of ants in San Francisco are categorized as generalist species and are not limited to a specific habitat.

Impact of Argentine ant on native species

Numerous studies have shown that Argentine ants displace native ants in California (Ward 1987; Majer 1994; Human and Gordon 1996, 1997; Suarez et al. 1998; Holway 1999; Laakkonen et al. 2001). Surprisingly, this study found no correlation between Argentine ant abundance and native species richness in parks, suggesting the impact of Argentine ants may be subdued here. This result may be explained by the low abundance of Argentine ants in many sampled parks. Pitfall traps failed to detect Argentine ants in fully half of parks sampled. In these parks, the Argentine ant's presence was confirmed by visual surveys, but individuals were only spotted around the perimeter of parks. These results suggest Argentine ants are largely confined to the edges of these parks. The low abundance of this species in San Francisco parks stands in stark contrast to a recent study conducted in urban parks in Australia. Walters (2006) found that 95% of ants in pitfall traps in invaded sites were Argentine ants, compared to 26% in this study. The differences between the two studies may be due to habitat type. Walters (2006) sampled in highly disturbed (mowed and watered with sprinklers) parks, whereas this study was conducted in more "natural" urban parks.

In traps that did contain Argentine ants, only four other species (*M. ergatongyna, P. imparis, T. andrei, and T. sessile*) were found, suggesting they can coexist with the Argentine ant. This has been supported by previous studies showing *T. andrei* and *P. imparis* to persist in areas with Argentine ants (Ward 1987; Human and Gordon 1996; Suarez et al. 1998). Suarez et al. (1998) suggested *T. andrei's* small size and cryptobiotic nature reduces competition for resources such as nesting space and food with the larger Argentine ant, which forages above ground. *P. imparis* tends to be more active in winter months (Tschinkel 1987), when Argentine ant activity is lower. Additionally, Holway (1999) documented that *M. ergatogyna* will use a highly repellent chemical defensive compound to fend off Argentine ants.

Implications for conservation

Urbanization is a serious threat to many of the rare and declining plants and animals in the San Francisco Bay area. Protecting and maintaining remaining urban natural areas not only helps conserve the city's biological diversity, but also provides valuable opportunities for human enjoyment. Conserving species in urban landscapes will depend on effective management planning, which includes both ecologically sensitive park design and the creation of a system of urban ecological reserves (Adams and Dove 1989).

The results of this study indicate that natural areas within urban parks play a critical role in supporting ant biodiversity. Many habitats in the natural areas of San Francisco's parks support healthy, diverse ant communities. Areas of non-native forest, however, reduce this diversity. Maintaining open grasslands, reducing tracts of non-native forest, removing the invasive understory, and thinning forest canopy may all help support a healthier ant community and ecologically valuable parks.

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Appendix 1

Table 6 List of parks surveyed, including summary of park characteristics

Park	Total Area (ha)	# of Habitats	Soil Moisture (%)	Irregularity index	Forest (%)	Grassland (%)	Scrub (%)	Mosaic (%)	# of pitfalls
Glen Canyon	24.28	7	3.36	2.13	29	23	39	3	117
Bayview	17.72	6	2.15	2.05	39	25	23	2	87
Mt. Davidson	16.15	6	15.65	1.52	75	12	8	4	76
Twin Peaks	11.86	7	3.68	5.04	3	18.7	36	35	57
Bernal Hill	9.75	6	2.70	2.95	6	82	2	2	44
Interior Green Belt	6.63	2	15.85	1.62	100	0	0	0	27
Golden Gate Park	5.22	3	8.92	2.89	98	2	0	0	25
Corona Heights	3.84	7	2.98	1.53	27	50	10	3	19
Pine Lake	2.75	3	6.85	1.72	48	0	29	0	14
Buena Vista Park	2.47	4	8.24	2.03	100	0	0	0	18
Hawk Hill	1.78	5	2.20	1.64	4.2	0	84.1	0	9
O'shaughnessy Hollow	1.74	4	2.13	2.02	0.4	22	67	0	7
Grandview Park	1.58	5	1.90	1.17	15	0	0	77.8	8
Billy Goat Hill	1.38	5	4.07	1.62	15	72	8	0	7
Tank Hill	1.13	5	4.77	1.21	19	55	17	0	6
Kite Hill	0.97	4	3.68	1.41	16	76	4	0	3
Edgehill Mountain	0.93	3	15.97	1.33	80.9	5.1	0	0	3
Palou Phelps	0.81	5	3.15	1.88	24	51	0	22	3
Brooks Park	0.77	6	4.65	1.75	15.1	59.6	0	10.9	4
Rock Outcrop	0.65	5	1.57	1.72	4.2	8.8	4.4	0	3
Golden Gate Heights	0.32	3	4.85	2.42	46.3	0	0	51.2	2
Fairmount Park	0.28	4	8.55	1.35	81	13.5	0	0	2
Lakeview Mini Park	0.16	3	2.60	1.48	0	75.6	0	0	2
15th Avenue Steps	0.12	3	2.65	1.71	48	0	48	4	2

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