

Increased abundance of native and non-native spiders with habitat fragmentation

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ABSTRACT

Habitat fragmentation and invasive species often contribute to the decline of native taxa. Since the penetration of non-native species into natural habitat may be facilitated by habitat fragmentation, it is important to examine how these two factors interact. Previous research documented that, in contrast to most other arthropod taxa, spiders increased in density and morphospecies richness with decreasing fragment area and increasing fragment age (time since insularization) in urban habitat fragments in San Diego County, California, USA. We tested whether a specific mechanism, an increase in non-native species with fragmentation, is responsible for this pattern. We found that both native and non-native taxa contributed to the pattern. Abundance of native spiders per pitfall trap sample increased significantly with decreasing fragment size (i.e. a negative density–area relationship) and abundance of non-natives increased significantly with increasing fragment age. The proportion of non-native individuals also increased significantly with age. One non-native species, *Oecobius navus*, comprised the majority of non-native individuals (82.2%) and a significant proportion of total individuals (25.1%). Richness of spider families per sample (family density) increased with fragment age due to an increase in the occurrence of non-natives in older fragments, however, native family richness did not vary with age or area. Due to increasing dominance by non-native and some native families, family evenness declined with decreasing fragment size and increasing fragment age. Native and non-native abundance covaried positively arguing against strong negative interactions between the two groups. *O. navus* had a strong positive association with another common non-native arthropod, the Argentine ant (*Linepithema humile*), suggesting a possible direct interaction. In contrast, abundance of native spiders was negatively correlated with Argentine ant abundance. We hypothesize that fragmentation in this semiarid habitat increases productivity in smaller and older fragments enhancing the density of both native and non-native taxa.

Keywords

Argentine ants, biological invasions, coastal sage scrub, habitat fragmentation, invasive species, non-native species, southern California, spiders, density–area relationship, *Oecobidae*, *Oecobius navus*.

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INTRODUCTION

The effect of habitat fragmentation on the abundance and diversity of vertebrates has received enormous attention. However, until recently there have been comparatively fewer studies of arthropod communities in habitat fragments (Kareiva, 1987; Kruess & Tscharrntke, 1994; Didham *et al.*, 1998a). In vertebrates the density and diversity of habitat interior species generally declines and that of edge species, habitat generalists, and non-native species often increases with decreasing fragment size (Bender *et al.*, 1998; Connor *et al.*, 2000). However, in arthropod studies these generalizations have found less support. Many

studies have demonstrated both increasing and decreasing arthropod density and diversity in habitat fragments as compared to unfragmented habitat (Fahrig, 2003; Ewers & Didham, 2006).

A number of theories predict that fragmentation should, in general, lead to reduced diversity and density of organisms, including arthropods. The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and metapopulation theory (Hanski, 1998) suggest that habitat fragmentation can reduce the diversity of organisms through increased probability of stochastic extinction and diminished recolonization. Diversity should also decline with fragment age as species number ‘relaxes’ to a lower equilibrium. Other theories that predict lower arthropod

species diversity and density with decreasing fragment size include: the resource concentration hypothesis (Connor *et al.*, 2000) and the habitat heterogeneity hypothesis (Ricklefs & Lovette, 1999). Habitat degradation, often associated with anthropogenic edges, also can lead to reduced diversity and density with declining fragment size and increasing fragment age (Harrison & Bruna, 1999).

Other theories address the attributes of species that influence fragmentation sensitivity. Food-web theory (Holt, 1996) suggests that predators are more vulnerable to habitat fragmentation than species at lower trophic levels. In experimental studies of habitat fragmentation on arthropods, predators and parasitoids have been shown to be more sensitive to fragmentation than herbivores (Kruess & Tschardtke, 1994; Didham *et al.*, 1998b). In urban forest fragments Miyashita *et al.* (1998) found web spider density and diversity declined with decreasing fragment size.

Recent theoretical and empirical studies suggest that density in fragments or natural habitat patches may either increase or decrease with patch area depending upon the relative importance of within-patch vs. between-patch processes. In populations dominated by between-patch processes the relative strength of scaling of immigration and emigration rates with patch area determine the sign of the slope between density and area (Hambäck & Englund, 2005; Hambäck *et al.*, 2007).

A variety of external influences, particularly those originating in the surrounding human-modified matrix can lead to increased arthropod diversity and density in fragments. Ecosystem productivity could be enhanced in fragments (Shochat *et al.*, 2004) or predation and parasitism decreased (Kruess & Tschardtke, 1994). 'Spillover' of species from the matrix habitat into fragments has been documented in a number of systems (Duelli, 1990; Shure & Phillips, 1991; Holway *et al.*, 2002a; With, 2002). In a highly modified matrix such as urban land-use, the matrix fauna may be dominated by abundant non-native species. Several studies have documented increased abundance of invasive, non-native arthropod species in smaller habitat fragments or along fragment edges (Suarez *et al.*, 1998; Hobbs, 2001; Ness, 2004). Thus, there is a potential interaction of two anthropogenic perturbations, habitat fragmentation and introduced species.

In a prior study, we documented that the density and diversity of most arthropod orders declined with decreasing fragment area and increasing fragment age (time since insularization) in urban habitat fragments in San Diego County, California, USA (Bolger *et al.*, 2000). There were, however, exceptions to this general pattern. Ground active spiders, in particular, increased significantly in density and morphospecies richness with increasing fragment age. There was a similar, although non-significant, trend of increasing density with decreasing fragment area. These results were surprising because they differed from the other taxa examined and were in contrast to many of the theoretical expectations listed above.

Here we test the hypothesis that this result is due to an increase in non-native spider species in smaller and older fragments. Prentice *et al.* (1998) and Burger *et al.* (2001) have demonstrated that the regional spider fauna in San Diego contains several

abundant non-native species. To test this hypothesis we re-examined the spider samples from Bolger *et al.* (2000) to classify them at a finer taxonomic level that allowed us to distinguish native from non-native taxa.

We also investigated the effect of another non-native arthropod on these spider communities. The non-native Argentine ant (*Linepithema humile*) invades native coastal sage scrub communities along urban edges in southern California (Suarez *et al.*, 1998; Bolger, 2007) and appears to contribute to the decline of most native ants. Argentine ants have become established in Mediterranean climates worldwide and have been implicated in the decline of native ants in many of those locations (reviewed in Holway *et al.*, 2002b; Rowles & O'Dowd, 2007). However, the effect of Argentine ants on non-ant arthropods is less clear. Several studies have implicated Argentine ants, or other non-native ants, in the decline of non-ant arthropods (Porter & Savigno, 1990; Cole *et al.*, 1992; Human & Gordon, 1997). Bolger *et al.* (2000) found negative associations between the abundance of Argentine ants and the abundance and diversity of a number of arthropod orders. Small-bodied, generalist ants such as the Argentine ant could compete with spiders as well as serve as spider prey. Here we examine the sign and strength of association between Argentine ants and native and non-native spiders.

METHODS

Study sites

The 39 fragments examined here, located in south-western San Diego County (Fig. 1), were also used in Suarez *et al.* (1998), and Bolger *et al.* (2000). See those papers for descriptors of individual fragments. Many of these were also used in previous studies of vertebrates (Soulé *et al.*, 1988; Bolger *et al.*, 1991, 1997; Bolger, 2002). Most are remnants of dendritic drainages that have been isolated by development sometime in the last 100 years. San Diego has a dry, Mediterranean climate and the predominant habitat type in these fragments is coastal sage scrub (henceforth CSS), a drought-deciduous shrub habitat, with smaller amounts of coastal chaparral (Alberts *et al.*, 1993).

Fragments ranged in total area from 0.4 to 102 ha and in age (years since insularization) from 3 to 95 years (as of 1995). The matrix is predominantly dense (6–18 residences per ha) single-family residential development (Bolger, 2001). These fragments are in landscapes with relatively small percentage of remaining habitat (*c.* 10%; Fig. 1). Several reviews have found the effects of fragmentation and edge to be most apparent in these types of landscapes (Andren, 1994; Fahrig, 1997).

Pitfall sampling

Samples were collected in arrays of five pitfall jars (250 mL jars, 60 mm inside diameter) placed at approximately 100-m intervals along a transect parallel to the longest axis of the habitat fragment (see Suarez *et al.*, 1998). Pitfall arrays were located in stands of native shrub vegetation and were distributed so that they varied in distance from the fragment edge. The number of arrays

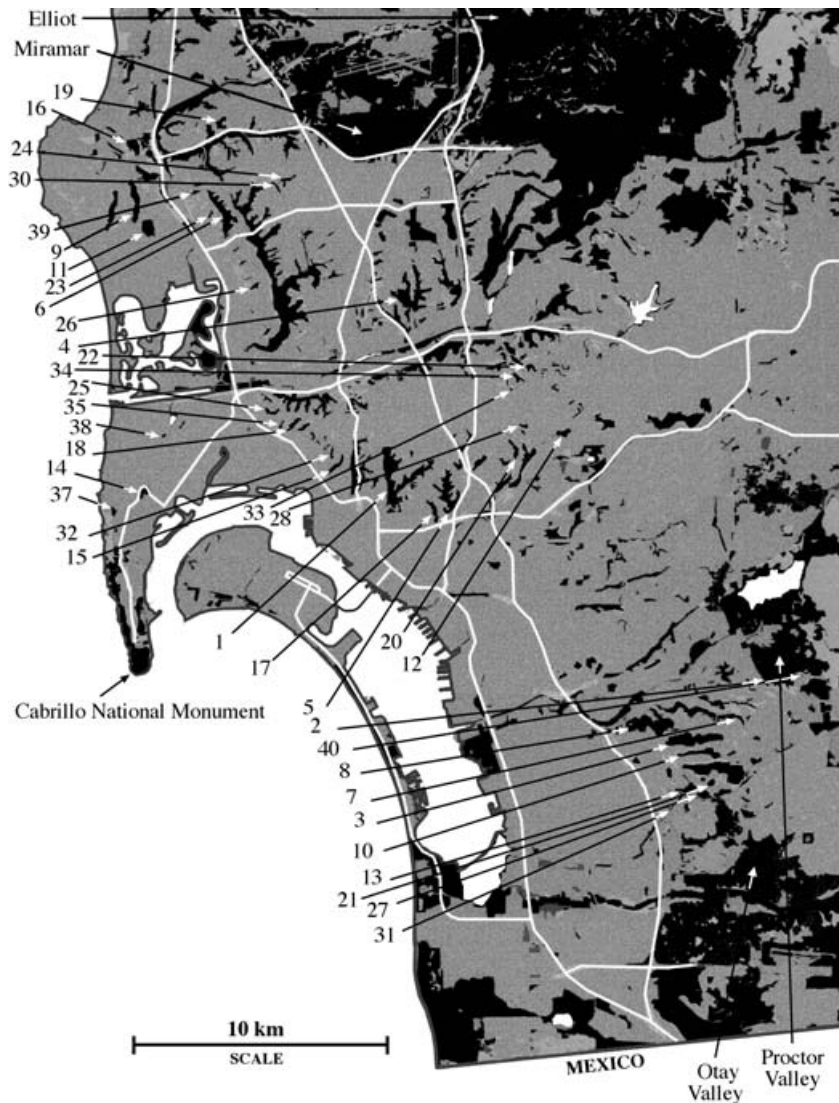


Figure 1 Map of habitat fragments studied in coastal San Diego County, California, USA. Numbers refer to fragment numbers in Table 1 in Bolger *et al.* (2000). The two fragments not shown on the map (Oak Crest and Montanosa) are located in Encinitas, approximately 10 km north of the map area. White lines indicate highways, grey background indicates urbanized areas, and black denotes areas with predominantly native vegetation.

varied with the size of the fragment and ranged from one to 11 per fragment with a mean of 3.9. The five jars in an array were placed in a pattern resembling the five on a die with the corner jars 20 m apart. Each jar was half-filled with a 50 : 50 mixture of water and non-toxic antifreeze. The antifreeze prevented evaporation and acted as a preservative. The jars were buried with the rim of the jar flush with the ground surface. All the jars in a fragment were opened for a five-day sampling period in the spring of 1996. The order of fragment sampling was randomized over a 2-month period, 1 May to 26 June, the season of highest arthropod abundance and activity in the region (Bolger *et al.*, 2000). The contents of the five jars in each array were pooled to form the sample for that point. Arthropods were separated from debris, washed, and stored in 70% ethanol. Data on the ants in these samples are reported in Suarez *et al.* (1998), and other arthropods in Bolger *et al.* (2000).

There were 150 individual locations sampled across the 39 fragments, each one with an array of five pitfall traps for 5 days, equalling a total of 3800 pitfall trap-days. The order of sampling

was random with regard to the variables important for our conclusions: area and age of fragments. Thus, our sampling was highly replicated in space and time at independent locations so our conclusions about the relationships documented here should be robust.

Pitfall trapping is probably the most cost-effective way of sampling and comparing ground-living spiders from different sites (Southwood, 1978). However, because taxa are not equally susceptible to capture, pitfall trapping introduces bias into invertebrate sampling (Southwood, 1978). Consequently, we use our data only to compare among sites, not among taxa. Our inferences about the effects of fragmentation are based on comparisons among these point samples, as is common in studies of factors influencing arthropod abundance and diversity (e.g. Didham *et al.*, 1998a; Ewers *et al.*, 2007). Thus, our inferences do not rely on the assumption that we are comparing a complete description of the spider assemblage in a fragment, but rather, that we are comparing equivalent samples of spider communities across fragments of different area and age.

The taxonomic richness of a point sample is determined by both the richness of the community being sampled as well as the overall spider abundance and thus the number of individuals captured. So the richness of point samples is a measure of 'species density' as defined by Gotelli & Colwell (2001). For simplicity we will refer to this as richness. The number of spiders captured in a pitfall trap is a function of the densities of individual species as well as their activity level and other dimensions of trapability. We refer to the number of spiders captured in each pitfall array as abundance per sample or simply point abundance. In the Discussion we will assume that this is a reasonable proxy for spider density and discuss our results in the context of other research on determinants of density in fragmented habitat.

Spider classification

Spiders in each sample were identified to family and morpho-species using eye shape and arrangement, leg spines, spinneret length, abdomen shape, and distinctive markings. All morpho-species were confirmed to family and were identified to genus or species (when possible) by Dr Thomas Prentice (Department of Entomology, University of California, Riverside). Samples were carefully examined for the presence of the seven non-native species known to occur in CSS in San Diego County from an extensive pitfall and vacuum sampling study (Prentice *et al.*, 1998). Since family was the lowest taxonomic level to which we could identify all individuals, we use this as the level at which we address the effect of fragmentation on spider diversity.

Fragment variables

Studies of the 'effects of habitat fragmentation' have interpreted that term in a variety of ways (Fahrig, 2003). As in many studies of fragmentation and arthropods we interpreted a change in the point diversity and abundance with fragment size as a consequence of habitat fragmentation. Furthermore, in this system, the age of a fragment, the years since insularization by development, has been shown to be a significant predictor of vertebrate diversity in fragments. Specialist vertebrates appear to go locally extinct in fragments over time (Soulé *et al.*, 1988; Bolger *et al.*, 1991, 1997; Crooks *et al.*, 2001). We assume that fragment age is a surrogate for the accumulation of disturbance and stochastic extinctions over time. So, we also consider patterns with fragment age to be a consequence of fragmentation. Fragment age (AGE) was determined from dated aerial photographs and building permit records (Soulé *et al.*, 1988; Suarez *et al.*, 1998). We used the area of native shrub vegetation in the fragment as our measure of fragment area (AREA) because it is a better measure of habitat area and a better predictor of coastal sage scrub arthropod, bird, and rodent diversity than is total fragment area (Soulé *et al.*, 1988; Bolger *et al.*, 1997, 2000). Preliminary analyses of the spider data confirmed that the same was true of spider abundance and diversity. Fragments range from 10% to 90% cover of coastal sage scrub and chaparral (Suarez *et al.*, 1998). The remaining area within each fragment was typically dominated by non-native grasses and forbs. Total fragment area was measured

from digitized, scaled aerial photographs taken in 1995. The percentage cover of native shrub vegetation was estimated by inspection of aerial photographs and vegetation surveys within each fragment (Suarez *et al.*, 1998). AREA was derived by multiplying the percentage cover of native shrub vegetation by total fragment area.

Sample point variables

At each pitfall array location, the following measures of local habitat variation were measured over a 20-m radius. The percentage cover of native shrubs (SHRUB), non-native nonwoody vegetation (EXOTIC), and the cover of each shrub species were classified using a Braun-Blanquet (Kent & Coker, 1992) categorical scale: 0 (< 1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (76–100%). Twelve common shrub species were scored for abundance: California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), Black sage (*Salvia mellifera*), California encelia (*Encelia californica*), lemonadeberry (*Rhus integrifolia*), laurel sumac (*Malosma laurina*), chaparral broom (*Baccharis pilularis*), manzanita (*Arctostaphylos glandulosa*), scrub oak (*Quercus dumosa*), chamise (*Adenostoma fasciculatum*), *Ceanothus* sp., and jojoba (*Simmondsia chinensis*).

A principal components analysis (PCA) was performed on the shrub species cover data. The scores from the first two axes (PC1 and PC2) were used in the multiple regression analyses described below. The first principal component separated sampling points that are typical coastal sage scrub from those with elements of Coastal Chaparral. PC1 loads heavily positively on chaparral shrub species (*Adenostoma fasciculatum*, *Arctostaphylos*, and *Ceanothus* sp.) and negatively on the coastal sage scrub species (*Artemisia californica*, *Encelia californica*, and *Rhus integrifolia*). PC2 separates sites that contained a mix of the chaparral species *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* with the coastal sage scrub species *Salvia mellifera*, *Artemisia californica*, and *Encelia* from sites that contain *Quercus dumosa*, *Malosma laurina*, *Heteromeles arbutifolia*, and *Baccharis pilularis*. The first two principal components captured 34% of the total variation in shrub composition of these sites. The relatively low explained variation reflects the high variation among sampling points in the relative abundance of these shrub species. This variation is likely due to slope, aspect, and edaphic factors as well as disturbance history. Further details of the PCA are in Bolger *et al.* (2000).

The Shannon–Wiener diversity index was also calculated from the shrub species data (SWDIV). Other variables measured included the distance from each sampling point to the nearest fragment edge (EDGEDIST) and the abundance of Argentine ants (AA) at each sampling point (data from Suarez *et al.*, 1998).

Analysis

Data were analysed at two spatial scales: among fragments and among sample points. As in previous studies of arthropod

diversity (Klein, 1989; Didham *et al.*, 1998a; Quintero & Roslin, 2005) we tested for a fragmentation effect by comparing the mean richness and abundance from multiple point samples within each fragment (mean point family level richness and abundance) among fragments. We compared among individual sample points to test for effects of the structure and composition of vegetation, edge proximity, and Argentine ants on native and non-native spider abundance per sample. All analyses were conducted with the JMP® statistical software (SAS Institute, Cary, NC, USA).

Among fragments – AREA and AGE multiple regression

To test for a fragmentation effect, we performed multiple regressions of the dependent variables, mean abundance per sample, mean family richness, and Shannon evenness (Magurran, 2004) of native and non-native spiders against the independent variables fragment AREA and AGE. All variables were log(base 10)-transformed except the proportion of non-native individuals which was arcsine square-root transformed and the evenness indices.

We also analysed the abundance per sample of the more common families individually. This included families whose mean abundance per sample averaged > 0.5 across fragments (Oecobiidae, Lycosidae, Gnaphosidae, Salticidae, Theridae, Dysideridae, Oxyopodidae, Tengelidae). Because the abundances of these families were non-normal and could not be normalized by transformation, they were analysed with bivariate nonparametric regressions.

Area and age were significantly correlated in this sample of 39 habitat fragments ($r = -0.43$, $n = 39$, $P = 0.006$). This is due in part to the tendency for fragment size to diminish with time since insularization as more of the fragment is developed and native shrub cover is lost to disturbance. Correlation among the independent variables, or collinearity, can cause instability in parameter estimates in multiple regression (Phillippi, 1993). To evaluate this possibility we removed the correlation by excluding four data points that had the highest leverage. This rendered the relationship between fragment age and area non-significant ($r = -0.16$, $n = 35$, $P = 0.35$). We then repeated all multiple regressions on this reduced data set. All results were qualitatively similar and parameter values nearly unchanged. In general, R^2 values were slightly higher and P -values slightly lower. We report only the regression results for the full data set.

Among sample points – multiple regression

To gain insight into the proximate factors that influence native and non-native spider abundance at the among sample point scale, we performed multiple linear regressions of abundance per sample on descriptors of vegetation and disturbance at each sampling site. The independent variables included a set that described the structure and composition of the woody vegetation (PC1, PC2, SWDIV, SHRUB) and a set that captured some elements of disturbance and edge effect (EXOTIC, EDGEDIST,

AA). To examine the possibility of negative interactions among non-native and native spiders, we also included the abundance per sample of non-native (with native abundance as the dependent) and native spiders (with non-native abundance as the dependent) in the analyses.

For these analyses we used only the sample points from the 11 fragments over 30 ha in total area. Smaller fragments are more likely to be dominated by among fragment scale variables such as AREA and AGE. Furthermore, smaller fragments have no 'interior' with regard to edge effects such as Argentine ant abundance (Suarez *et al.*, 1998). For instance, all sample points in smaller fragments have moderate to high abundance of Argentine ants, while many points in the interior of larger fragments have low to no Argentine ants. Restricting ourselves to the larger fragments restricts the range of the among fragment variables such as AREA and AGE yet maintains the range of the among sample point disturbance variables EDGEDIST, AA, and EXOTIC, thus helping to isolate those effects. The dependent variables and EDGEDIST and AA were log(base 10)-transformed to conform to regression assumptions.

Rarefaction

Differences in taxonomic richness among biodiversity samples can be due both to differences in the underlying community richness as well as in community abundance that influences the number of individuals in the sample and thus the richness (Gotelli & Colwell, 2001). We found differences with fragment age in both richness and abundance (see Results), so to help determine the effect of sample abundance on sample richness we performed rarefaction using EstimateS (Colwell, 2006). The pitfall samples were divided into two categories for rarefaction, those from fragments older than 30 years and those from fragments younger than 30. This roughly divided the number of samples evenly, 68 samples (1423 individuals) for older fragments and 82 samples (1077 individuals) in younger fragments.

RESULTS

A total of 2539 spiders were captured, 2500 were identified at least to family and 1387 were identified to genus or species. Spiders from 31 families were identified (see Appendix S1 in Supplementary Material). Five non-native species were found to be present (*Metaltella simoni*, *Dysdera crocata*, *Trachyzelotes lyonneti*, *Zelotes nilicola*, *Oecobius navus*) and comprised 31% of all spider individuals. Three families were represented by single, non-native species: Oecobiidae (*O. navus*), Amaurobiidae (*M. simoni*), and Dysideridae (*D. crocata*). The two other non-native species (*T. lyonneti* and *Z. nilicola*) are in the family Gnaphosidae and could be reliably distinguished from the native species in that family.

Oecobius navus was by far the most common species, comprising 25.1% of all spider individuals and 82.2% of the non-native individuals. Individual pitfall samples ranged from 0 to 84% non-natives. At the level of whole fragments, non-native spiders averaged 27% of all spiders captured (range 0–68%).

Table 1 Results of multiple regression analysis of the abundance and family richness per pitfall sample of native and non-native spiders, and the non-native species, *Oecobius navus*, on fragment area and age. Standardized partial regression coefficients and *P*-values are given as well as *P* and adjusted *R*² for the model.

Dependent variable	Area	Age	<i>R</i> ² adjusted	Model <i>P</i>
Total abundance	-0.21	0.58****	0.46	<0.0001
Native abundance	-0.33*	0.28†	0.23	<0.01
Non-native abundance	0.15	0.71****	0.41	<0.0001
<i>O. navus</i> abundance	0.16	0.75****	0.45	<0.0001
Family richness	0.12	0.53**	0.20	<0.01
Native family richness	0.16	0.30	0.02	0.26
Non-native family richness	0.13	0.61***	0.29	<0.001
Proportion non-native individuals	0.17	0.22**	0.22	<0.01
Family evenness	0.05	-0.45**	0.18	<0.01
Native family evenness	0.28†	-0.31†	0.21	<0.01

†0.1 > *P* > 0.05; **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *****P* < 0.0001.

Patterns with fragment area and age

The total abundance per sample of spiders increased significantly with increasing fragment age (Table 1). The native component of abundance increased significantly with decreasing fragment area (Fig. 2a, Table 1) and showed a non-significant increasing

trend with increasing fragment age (Fig. 2d). The abundance per sample of non-native spiders was not significantly related to area (Fig. 2b), but increased significantly with increasing fragment age (Fig. 2e, Table 1). The dominant non-native species, *O. navus*, also showed no relationship with fragment area (Fig. 2c), but increased significantly with fragment age (Fig. 2f, Table 1).

Total family richness increased significantly with increasing fragment age, however, native family richness (total family richness minus families represented in that sample by only a non-native species) showed no relationship with either age or area (Table 1). Non-native family richness increased significantly with increasing age.

Consistent with the greater increase in non-native than native abundance per sample with fragment age, the proportion of all spiders captured that were non-natives increased significantly with age but not with area (Table 1). Due to the increasing dominance by *O. navus*, as well as native families, family evenness declined significantly with increasing fragment age (Table 1). Considering only families represented by native species, there was still a non-significant trend towards decreasing evenness with increasing age and decreasing area. The increasing dominance in older fragments was also supported by rarefaction (Fig. 3). Although the confidence intervals (CI) of the two rarefaction curves were broadly overlapping (95% CI at 900 individuals were 18.9–28.6 for older fragments and 21.0–31.4 for younger fragments), the trend was that younger fragments supported greater family richness for a given number of individuals sampled.

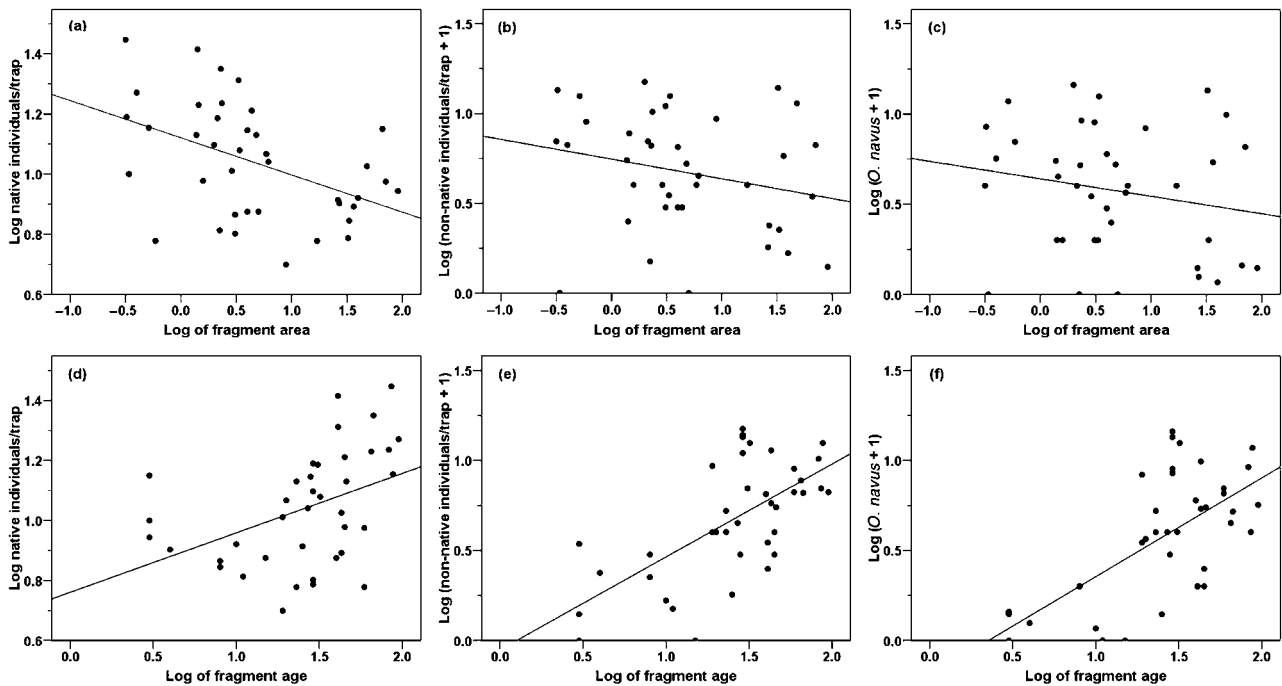


Figure 2 Regressions of mean native spider abundance per pitfall sample per fragment against fragment area (a) and age (d), mean non-native spider abundance per pitfall sample per fragment against (b) fragment area and (e) age, mean abundance per pitfall sample per fragment of the dominant non-native species, *Oecobius navus*, against (c) fragment area and (f) age.

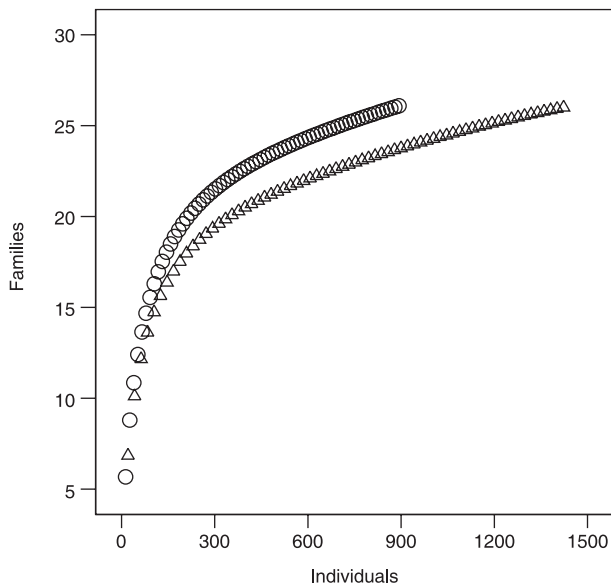


Figure 3 Rarefaction of family richness of spider pitfall samples. Triangles are from pitfall samples from fragments greater than 30 years old and circles are samples from fragments less than 30 years old.

Patterns with individual families

Among the individual families, the Oecobiidae (including only the non-native *O. navus*) showed a strong increase with fragment age (Table 2). The only other family to show significant relationships was Lycosidae, which increased with age and declined with area. Gnaphosidae and Oxyopodidae displayed near significant relationships to fragment area with oxyopodids increasing with area and gnaphosids decreasing. The oxyopodids were the only family to show a trend towards increasing abundance per sample with increasing area (Table 2).

Among sample point patterns

At the among sample point scale, a significant regression model was fit for the abundance of native spiders, but the model fit was relatively poor (Table 3). There were significant associations between native spider abundance per sample and Argentine ant abundance (negative), non-native spider abundance (positive), and PC1 (negative). The model fit for non-native abundance per

Table 2 Non-parametric, bivariate correlations of the abundance per pitfall sample of individual spider families with fragment area and age.

Dependent variable	Independent variable	Spearman Rho	P
Oecobiidae	Log area	-0.175	0.29
Lycosidae	Log area	-0.466	<0.01
Gnaphosidae	Log area	-0.290	0.07
Salticidae	Log area	0.086	0.60
Theridae	Log area	-0.166	0.31
Dysderidae	Log area	-0.192	0.24
Oxyopidae	Log area	0.287	0.08
Tengeliidae	Log area	0.039	0.82
Oecobiidae	Log age	0.588	<0.0001
Lycosidae	Log age	0.690	<0.0001
Gnaphosidae	Log age	0.050	0.76
Salticidae	Log age	-0.049	0.77
Theridae	Log age	-0.008	0.96
Dysderidae	Log age	0.158	0.34
Oxyopodidae	Log age	0.013	0.94
Tengeliidae	Log age	0.198	0.23

sample was better. They were positively associated with PC1 (an indicator of the presence of chaparral shrub species), with the abundance of Argentine ants, and with the abundance of native spiders. When only the dominant non-native, *O. navus*, was analysed, model fit was somewhat higher and there were again significant positive associations with PC1, Argentine ants, and native spiders.

DISCUSSION

Our results indicate that the density of both native and non-native spiders is enhanced by the process of urban habitat fragmentation in San Diego, CA, USA. Non-native species increased strongly in abundance per sample with increasing fragment age, while native spider abundance per sample increased significantly with decreasing fragment area and marginally significantly with increasing fragment age (Table 1). Thus, the increase in abundance in older fragments was mostly due to non-native species, principally *O. navus*. However, higher abundance in smaller fragments was mainly attributable to native taxa. Thus the observed increases in spider abundance per sample with decreasing

Table 3 Results of multiple regression analysis of spider abundance per pitfall sample against descriptors of within-fragment habitat variation. Standardized coefficients and *P*-values are given as well as *P* and *R*² for the model; *n* = 64. Independent variables are described in the text.

Dependent variable	Adj. <i>R</i> ²	Model <i>P</i>	AA	Native abundance	Exotic abundance	PC1	PC2	SWDIV	EXOTIC	EDGE DIST	SHRUB
Native abundance	0.16	0.02	-0.37*	-	0.37*	-0.36*			0.25†	0.29†	
Exotic abundance	0.35	<0.0001	0.30*	0.29*	-	0.42**					
<i>Oecobius navus</i> abundance	0.39	<0.0001	0.35**	0.22*	-	0.59***					

†0.1 > *P* > 0.05; **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *****P* < 0.0001.

fragment area and increasing age observed by Bolger *et al.* (2000) were not solely due to a positive response of non-native taxa to fragmentation, but were a product of the responses of both native and non-native taxa. Due to the strong increase in non-natives in older fragments, the proportion of non-native individuals increased significantly with increasing fragment age (Table 1).

The response of family level richness per sample was not as strong as that of abundance. Total family richness per sample increased significantly with fragment age. When diversity was partitioned among non-native and native family richness, non-native family richness increased significantly with fragment age but native family richness showed no relationship with age or area (Table 1). Thus, increases in family richness seem to be solely due to increased occurrence of non-native families.

The evenness of family abundance declines significantly with increasing fragment age (Table 1) due, in part, to the pronounced increase of non-native spiders, particularly *O. navus*, with fragment age. However, it is not completely a non-native phenomenon. When the non-native families are removed, there is still a nearly significant trend to reduced native family evenness with increasing age and decreasing area (Table 2). The abundance of several wholly native families, particularly Lycosidae, tended to increase with fragment age and decline with fragment area (Table 2), contributing to the decline in evenness. This decline is also reflected in the rarefaction analysis that suggests that higher richness in the samples from older fragments is due only to the increased abundance per sample; on an equal abundance basis, samples from younger fragments tend to contain higher family richness (Fig. 3).

Thus, the increasing dominance of *O. navus* as well as native taxa leads to homogenization (McKinney & Lockwood, 1999) of the spider fauna in older and smaller fragments. Faunal homogenization has often been observed in urban and urban-influenced habitat (Marzluff, 2001; Shochat *et al.*, 2004) where total faunal density often increases but diversity is much lower than in nearby natural habitat. Our results are unique in that typically the homogenization is due to both reduced native diversity and density and increased non-native or synanthropic species, whereas here native density has increased and there is no discernable decline in native diversity at the family level.

Species at higher trophic levels are thought to be more vulnerable to local extinction in small, isolated habitat fragments because of lower density and thus smaller population sizes (Holt, 1996). However, we found spider diversity and density enhanced in smaller and older fragments. One interpretation of our results is that spider density and diversity are not driven by between-patch processes of extinction and colonization but are more a function of within-patch processes such as ecosystem productivity. We hypothesize that the pattern we observed results from a bottom-up response to increased productivity in small fragments. Spiders are often food-limited (Wise, 1993), thus an increase in ecosystem productivity would be expected to lead to increased density. Ecosystem productivity may be higher in smaller and older fragments for several reasons. In this semiarid region (UNEP, 1992) plant productivity is generally water limited, as are secondary and tertiary productivity (Bolger *et al.*, 2005). We

believe that water limitation is ameliorated in smaller and older fragments through several mechanisms. Small fragments have higher edge-area ratios and thus may receive higher water subsidies due to surface run-off from impervious surfaces and irrigation run-off (Holway *et al.*, 2002a). Smaller fragments have a greater number of non-native trees in and adjacent to the fragment (Crooks *et al.*, 2004). The shade provided by these trees in these open shrub habitats should lead to lower air and soil temperatures, and higher relative humidity and soil moisture.

Similar relationships between productivity and spider abundance have been documented in other arid and semiarid region studies. Burger *et al.* (2001) found a gradient in total spider abundance with distance to the coast in San Diego County. Abundance of both non-native and native spiders was higher closer to the coast in more mesic, presumably more productive sites. Spider abundance did not vary with distance to the coast in our data set (D.T.B., unpublished data). Our sites occurred within a similar range of distances from the coast (1–17 km) to theirs (1–22 km). But, they had many more sites within 1–2 km of the coast (14 of 60), while we had few (2 of 39). Shochat *et al.* (2004), also in an arid environment, found higher spider abundance in more mesic, human-modified habitats. But in contrast to our results they found diversity was lower in those habitats compared to more natural, xeric habitats.

Another contributing mechanism could be vegetation changes that occur as fragments 'age'. In older fragments, cover of perennial woody plants is lower, and cover of non-native annual grasses and forbs is higher than in younger fragments (Alberts *et al.*, 1993). The nutrients in these annual plants turn over more rapidly than do those in woody plants (Jackson *et al.*, 1988) and probably fuel a more productive detrital food chain that may support higher spider densities (Chen & Wise, 1999). Alternatively, this change in the structure of the vegetation could affect spider density and diversity directly (Borges & Brown, 2001).

The response of several individual families parallels that of other recent studies in the south-west USA. Shochat (2004), working in urban habitats and desert remnants in Phoenix, Arizona, found that high productivity urban habitats were dominated by Lycosidae. Wenninger & Fagan (2000) compared three urban riparian zones in Phoenix and found lycosids to be most diverse and numerous at the site with highest soil moisture. Both of these studies support our hypothesis that moisture and productivity drive patterns of spider abundance and diversity in fragments. The one family that showed a negative response to fragmentation in our study, the Oxyopidae, crab spiders, was absent from high productivity sites in the study by Shochat *et al.* (2004).

Several alternative explanations for our results need to be evaluated. Arthropods sometimes increase in diversity with fragmentation because of 'spillover' of species that specialize on the matrix habitat (Duelli, 1990; Shure & Phillips, 1991), or because generalist species may be positively affected by fragmentation and outweigh the negative impacts on specialists (Didham *et al.*, 1998a). We have not sampled in the matrix habitat and so cannot evaluate the spillover hypothesis. Also, not enough is known about the ecology of the spider fauna to allow us to separate

generalist and specialist taxa. Consequently, these patterns may reflect the differing responses of generalist and specialist species.

We have not measured immigration and emigration rates and thus cannot rule out the possibility that these could be stronger influences than within-patch productivity. In systems dominated by among-patch processes, Hambäck & Englund (2005) have shown that the slope of the density–area relationship depends on the relative scaling of immigration and emigration rates. To produce a negative density–area relationship, such as we see here, per capita immigration must decline more strongly with patch area than does emigration. The dispersal mechanisms of spiders suggest that immigration and emigration rates would be area-independent and thus unlikely to create this negative slope. Long-distance dispersal in spiders is usually accomplished by ballooning (Weyman, 1993). Since this is a passive mechanism of dispersal the number of emigrants and immigrants should be directly proportional to area and thus produce a density–area relationship with slope of zero.

At the among sample-point scale, abundance of native and non-native spiders positively covaried (Table 3). This argues against strong negative interactions between these two groups of spiders. It suggests that more diverse native spider communities do not resist invasion by non-natives and that abundant non-natives do not competitively exclude natives. However, these non-experimental results do not allow us to rule out the existence of these negative interactions; they could be masked by stronger positive covariance of abundance in both groups with environmental variation (Schoener & Adler, 1991). Burger *et al.* (2001) also found positive covariance between native and non-native spiders in San Diego.

Association of non-native spiders and ants

The abundance of the non-native spider *O. navus* is striking and is responsible for the decline in family evenness with increasing fragment age. *Oecobius navus* is a cosmopolitan, synanthropic species, possibly of African origin (Shear & Benoit 1964, cited in Santos & Gonzaga, 2003) that is widely naturalized in the south-western USA. It is small-bodied (2–3 mm) and builds webs of about 1 cm diameter (Shear, 1970; Gaston *et al.*, 1972). Burger *et al.* (2001) also found *O. navus* to be common in San Diego. It comprised 16% of all spiders in their samples compared to 25% in our samples. (note: *O. navus* was misidentified as *O. annulipes* in both Burger *et al.*, 2001 and Prentice *et al.*, 1998; T. Prentice, pers. comm.)

The strong positive association of the non-native *O. navus* with the non-native ant, *L. humile*, suggests an ecological link between these species. We have no observational evidence on whether this represents an interaction between the species (facilitation or a predator–prey relationship) or simply a similar response to environmental variation. However, several sources cite ants as the dominant prey of spiders in this genus (Glatz, 1967; Gertsch, 1979). Gertsch (1979) reports that *O. navus* feeds primarily on ants, flies, and other small insects. Argentine ants are in the size range (2.5 mm) of known prey of *O. navus*. Based on the natural history of this species and our correlational data,

we hypothesize that *O. navus* prey on Argentine ants and thus their abundance is increased in areas of high Argentine ant abundance.

In contrast, native spiders are negatively associated with Argentine ants (Table 3). Argentine ants are associated with habitat edges in these fragments (Suarez *et al.*, 1998; Bolger, 2007), thus, it is not surprising that we also observed a trend towards higher native spider abundance at greater distance from the fragment edge (Table 3). Both Cole *et al.* (1992) and Human & Gordon (1997) report negative associations of Argentine ants and spiders and suggest they may compete for prey. Bolger *et al.* (2000) found negative associations between Argentine ant abundance and that of a number of taxa that are also common prey of spiders. Of course, these correlational data do not allow us to evaluate the alternative direct and indirect pathways that could lead to this pattern of associations between Argentine ants, native spiders, and non-native spiders. Given the ubiquity and ecological importance of these taxa in fragmented habitat in southern California (Prentice *et al.*, 1998; Suarez *et al.*, 1998), these relationships warrant further examination.

These results may reflect a general difference between the consequences of habitat fragmentation in semiarid and arid as compared to mesic habitats. It is likely that, due to irrigation, the productivity of the human matrix in arid environments is higher than that of the adjacent natural habitat. This is probably less true in mesic regions, for instance, those that support forest. Thus, fragmentation in arid environments may typically create a productivity supplement to habitat fragments.

ACKNOWLEDGEMENTS

This research was supported by NSF grants DEB99-81758, DEB-0316798 to DTB, and DEB-0516452 to AVS. T. Prentice, A. Graham, K.L. Muse, and M. Thering provided assistance in sample processing and species identification. T. Crist and R. MacNally provided insightful comments on the manuscript.

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Editor: Ralph Mac Nally

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Spider families and number of captures in pitfall traps in urban habitat fragments in San Diego, California, USA.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2008.00470.x>

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