Evidence for spider community resilience to invasion by non-native spiders

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Abstract

The negative impacts of non-native species are well documented; however, the ecological outcomes of invasions can vary widely. In order to determine the resilience of local communities to invasion by non-native spiders, we compared spider assemblages from areas with varying numbers of non-native spiders in California coastal sage scrub. Spiders were collected from pitfall traps over 2 years. Productive lowland coastal sites contained both the highest proportion of non-natives and the greatest number of spiders overall. We detected no negative associations between native and non-native spiders and therefore suggest that non-native spiders are not presently impacting local ground-dwelling spiders. Strong positive correlations between abundances of some natives and non-natives may be the result of similar habitat preferences or of facilitation between species. We propose that the effects of non-native species depend on resource availability and site productivity, which, in turn, affect community resilience. Our results support the contention that both invasibility and resilience are higher in diverse, highly linked communities with high resource availability rather than the classical view that species poor communities are more invisible. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Non-native species frequently pose a threat to the persistence of natives, presumably through competitive exclusion or predation. Several examples of the devastating, community-wide effects of introduced organisms exist (e.g., Enserink, 1999, Strayer, 1999), but these examples represent extreme cases. More commonly, we encounter non-native species seemingly coexisting with natives, and for the most part we are unaware of their effects (Aniansson, 1999).

Non-native organisms potentially exert four distinct types of effects on a native species or community. They may (1) impact and degrade an entire community or ecosystem; (2) cause declines in specific, possibly unrelated, native species or small sets of unrelated species (presumably through competition or predation); (3) cause declines in closely related taxa (most likely through competition); or (4) have no discernible effect on population levels (but may or may not alter foraging behavior, habitat choice, etc.). That an entire ecosystem can be affected, directly or indirectly, by an exotic species is exemplified by such classic cases as the brown tree snake Boiga irregularis in Guam (Fritts and Rodda, 1998), the red imported fire ant Solenopsis invicta in Texas (Porter and Savignano, 1990), and cheatgrass Bromus tectorum in shrub-steppe vegetation (Brandt and Rickard, 1994). The effects that non-native species can have on populations of unrelated species have also been documented, as with European Starlings Sturnus vulgaris outcompeting nesting Northern Flickers Colaptes auratus (Ingold, 1996) and Purple Martins Progne subis (Brown, 1997). Reports of negative effects on populations of related species are numerous. The non-native crayfish Orconectes rusticus outcompetes native Orconectes species in Wisconsin (Hill and Lodge, 1999), bullfrogs Rana catesbiana deplete populations of native Rana species throughout California (Hayes and Jennings, 1986), and Argentine ants, Linepithema humile, depress many native ant species’ populations along urban interfaces in California (Holway, 1999, Suarez et
al., 1998). Published cases of exotics not affecting natives are less common (Bauchau, 1997), but do exist. For example, non-native fishes in some streams of northern California are not significantly changing native species assemblages (Baltz and Moyle, 1993), in contrast to their effects in other regions of North America (Moyle, 1995, Chapleau et al., 1997).

It is thus difficult to predict the degree to which non-natives are able to invade ecosystems. Elton (1958), MacArthur (1970), Stachowicz et al. (1999) and others proposed that species-poor ecosystems are most easily invaded. Such systems contain species depauperate communities that may reflect low resource availability or high levels of disturbance and result in a less efficient utilization of resource space. However, the bulk of experimental data suggest the opposite trend: areas of high diversity are more likely to support invading species (Levine and D’Antonio, 1999, Levin, 2000). Diversity may reflect high resource availability, high productivity, and high structural complexity.

Similar disagreement exists as to which conditions most favor large scale effects on resident fauna (Levine and D’Antonio, 1999). Whatever the optimal conditions for invasion and establishment may be, it is certain that habitat fragmentation and anthropogenic influences increase both the likelihood of invasion and the severity of the invaders’ effects on natives (Enserink, 1999). We have studied geographic patterns in local spider assemblages in order to determine which of these processes may apply to ground-dwelling spider communities in southern Californian coastal sage scrub (CSS) habitats.

CSS is a major vegetation type in cismontane southern California (Westman, 1981). Its canopy is composed of drought-deciduous shrubs such as Artemisia californica (Asteraceae) and Eriogonum fasciculatum (Polygonaceae). Its understory was historically composed of a rich array of native annual forbs. Primarily as a result of urban development, associated changes in fire frequency, and increased pollution, CSS has become increasingly fragmented and vulnerable to invasion by non-native plant and animal species (Westman, 1979, Zedler et al., 1983, Styinski and Allen, 1999). Both non-native grasses (e.g. Bromus spp., Avena spp.) and annual forbs (e.g. Erodium spp., Centaurea solstitialis) are now common in most CSS and are threatening native species’ persistence (Eliason and Allen, 1997). To our knowledge, only one invasive arthropod species, the Argentine ant, has been studied in CSS. This species outcompetes and eliminates native ants in CSS within valleys along urban edges (Suarez et al., 1998).

CSS contains a diverse spider fauna whose species composition and response to non-native invasion is largely unknown. We have documented over 200 spider species from CSS vegetation in San Diego County (Prentice et al., 1998). Of these species, seven are non-natives that have become established in southern California within the last 100 years (Chamberlin and Ivie, 1935, Gertsch, 1979, Platnick and Shadab, 1983, Platnick and Murphy, 1984). Four of these seven are gnaphosids, the most abundant and diverse group of native ground-dwelling spiders in CSS (Prentice et al., 1998). They represent a single guild (sensu Root, 1967) of wandering, generalist predators. One, Dysdera crocata (Dysderidae), is an isopod specialist (Gertsch, 1979). Another, Oecobius annulipes (Oecobiidae), is a small, relatively sessile web-builder. Yet another, Metalatta simoni (Amphibientidae), is a moderately large ground dweller.

Based on generally accepted theory, if the hypothesis of higher invasibility of low diversity sites is true, then sites with lower species richness should have more non-natives (and, by corollary, vice versa). Thus, our objectives were (1) to describe the pattern of occurrence of non-native spiders across sites in CSS, (2) to determine the degree of association between native spiders, non-native spiders, and their environment, and (3) to study the intraguild relationships between closely related native and exotic gnaphosid spiders. We predicted that, if non-natives were impacting native spider communities, their effects would be most obvious within the ecologically and behaviorally similar gnaphosids.

2. Methods

2.1. Field collection and identification

In order to describe patterns of abundances of native and non-native spiders, we sampled spiders from 60 sites in undisturbed CSS and chaparral intergrades across coastal San Diego County, California, USA. Sites were located at Marine Corps Base Camp Pendleton and Marine Corps Air Station Miramar (Prentice et al., 1998). Spiders were collected during 1-month sampling periods in December 1994 and 1995, May 1995 and 1996, and August 1995 from five randomly placed 473 ml (16 oz.) pitfall traps at each site. Traps remained in place for the duration of the study. Collection cups contained a dilute aqueous solution of Alconox detergent and salt to increase miscibility and decrease decay. Pitfall traps have been shown to be effective when estimating cursorial spider (and other arthropod) fauna richness and activity (Uetz and Unzicker, 1976) and are currently the most accepted method for conducting ecological studies on these species. Traps were left open for 7 days during each collection period. All mature (and distinct immature) spiders collected were identified to species by Prentice. All immature morphospecies that could not be identified to a distinct genus or species with certainty were eliminated from the data set (17% of all morphospecies; 15% of all spiders).
Taxonomy and nomenclature of Araneae follows Platnick and Murphy (1998).

A single adult of the non-native gnaphosid Trachyzelotes barbatus (first San Diego County record, see Platnick and Murphy, 1998) and of Metalatta simoni were collected. These records were eliminated from Mantel and detrended correspondence analyses (see below), because they could not reflect patterns of occurrence. Several immature Trachyzelotes that could not be identified to species also were collected. As no native Trachyzelotes are known from North America (Platnick and Murphy, 1984) and we collected only one other Trachyzelotes species in our study, all immature Trachyzelotes were considered to be the more commonly collected Trachyzelotes lyonetti. In total, we analyzed the patterns of occurrence of 145 spider species, including the five non-native species for which we had sufficient sample. All data were pooled across years and seasons in order to examine overall effects on species numbers and to minimize the number of zero values in any particular sampling period.

We measured vegetation and geographic variables at all sites to describe and account for the pattern of native and non-native spider species occurrence explained by local habitat conditions. Transects were established at fixed locations within each plot and vegetation was recorded in April–May 1995 from a total of 95 points placed randomly at 2-m intervals along transects using a point-transect method. From these measurements we obtained cover estimates for forbs, grasses, leaf litter, and shrubs. We also measured distance to coast, aspect, and elevation using standard GIS software (ArcView, ver. 3.2, 1999, ESRI) and electronic maps provided by Marine Corps Base Camp Pendleton and Marine Corps Air Station Miramar. Collectively, we refer to the vegetation and geographic measurements as environmental parameters.

2.2. Analyses

We used the presence or absence of non-natives at sites in \( \phi \) correlations (Sokal and Rohlff, 1995) to determine whether non-native spiders tended to co-occur. Significance levels were adjusted using a Dunn-Šidák \( [z' = 1-(1-\alpha)^{1/k}] \) correction for \( k \) multiple comparisons (Sokal and Rohlff, 1995).

We tested for similarity in pattern of occurrence between native and non-native species groups using a Mantel test (Douglas and Endler, 1982; PC-ORD, ver. 3.0, 1997, MJM Software) that compared Jaccard similarity matrices of species presence/absence. We expected that native species assemblages would be negatively associated with non-natives. Values in the non-native presence/absence matrix were transformed by adding 1 to avoid a divide-by-zero error for sites that contained no non-natives.

We used detrended correspondence analysis (DCA; Hill and Gauch, 1980; using PC-ORD) to investigate whether the composition of native spider communities (presence/absence of species) changed across an environmental gradient and whether that gradient corresponded to the level of invasion by non-natives. We identified three levels of invasion based on natural breakpoints in non-native abundance at sites: ‘low’ with 0–14 non-native individuals, ‘med’ with 15–50 individuals, and ‘high’ with 60–148 individuals. DCA axis scores were correlated (using Pearson product-moment correlations) with environmental parameters (as defined above). Those parameters most highly correlated with axis scores were used to identify axes 1 and 2.

We used logistic regression (Sokal and Rohlff, 1995; SAS Statistical Software, ver. 6.13, 1997) to account for environmental effects on variation in the proportion of natives before testing for the association between natives and non-natives that was independent of environment. We transformed (arcsine square-root) the environmental variables represented by grass, forb, litter, and shrub cover frequencies to normalize their distributions. Other variables (distance to coast, elevation, and aspect) were not transformed. Our baseline model used all environmental variables as a predictor of native species proportion. Once constructed, we used log-likelihood ratio tests to investigate the degree to which each non-native species increased the predictive power of the model built from environmental variables. All environmental variables were retained in the model in order to maximize the variance explained in the proportion of natives at sites. If an exotic species did not add to the power of the model predicting the proportion of natives, we would conclude that that species had no significant detectable effect on natives.

Finally, we used Pearson product–moment correlations to look for associations between abundances of native and non-native gnaphosids (omitting species that occurred in fewer than four sites). Significance levels were adjusted using a Dunn-Šidák correction.

3. Results

3.1. General patterns for non-native spiders

Non-native spiders occurred on 51 of the 60 sites sampled. At eight sites they constituted more than 50% of all spiders collected (Fig. 1). Occurrences of the non-natives Urozelotes rusticus and Dysdera crocata were highly correlated with one another (\( \phi = 0.41, P < 0.01, z' = 0.01 \)). Both species tended to occur in more coastal, mesic sites. Dysdera crocata occurrence was also correlated with that of Oecobius annulipes (\( \phi = 0.14, P < 0.01, z' = 0.01 \)); both species tended to occur in lowland and valley sites. Oecobius annulipes, a cosmopolitan
species that has colonized undisturbed habitats across the Southwest (Shear, 1970, Prentice et al., 1998), was the most common spider collected from pitfalls (comprising 16% of all spiders). It was most abundant at low elevation coastal sites.

3.2. Association between natives, non-natives, and environment

Although native species richness was uncorrelated with non-native abundance (Fig. 2), associations between the two groups emerged. Contrary to our expectations, we found a significant positive association between native and non-native species groups occurring on sites (Mantel standardized $r = 0.29$, $P = 0.001$). When native-only species assemblages on sites were compared by DCA, they were ordered along a gradient associated with litter cover as well as with distance to coast and associated changes in elevation (Fig. 3). Sites containing high numbers of non-natives clustered together and occurred at the low end of the gradient for litter. However, those containing medium or low/no numbers of non-natives remained unordered with respect to either litter cover or distance to coast.

Fig. 1. Proportion of non-native spiders collected from pitfall traps. Spiders were collected at sites within (A) Marine Corps Base Camp Pendleton, and (B) Marine Corps Air Station Miramar, San Diego County, California ($n = 60$ sites).
Using a logistic regression model, the proportion of native species occurring on sites could be predicted with our chosen environmental parameters ($\chi^2 = 51.56$, d.f. = 7, $P < 0.001$). Distance to coast was the only parameter that contributed significantly to the model (Wald’s $\chi^2 = 17.76$, d.f. = 1, $P < 0.001$, $\alpha' = 0.001$); however, it was strongly correlated with elevation. Distance to coast also was significantly negatively correlated with both overall spider abundance and the proportion of non-native spiders (Fig. 4a,b).

Once we accounted for the effects of environmental variables on the presence of native spiders, we assessed whether exotic spider species were associated with the occurrence of natives. Each non-native species was added in turn to the above logistic model and tested for improvement in the model $R^2$. By so doing, we tested for associations between species that were independent of their association with a particular habitat. Only the abundance patterns of *Dysdera crocata* and *Oecobius annulipes* significantly increased the predictive power of the logistic model (Table 1). After we accounted for the effect of the environmental variables, based on their parameter estimates, both species were positively associated with the proportion of natives.

### 3.3. Intraguild associations between native and exotic gnaphosids

The Gnaphosidae were the most diverse family of spiders collected, represented by 22 species, of which four were non-native. Because of their diversity and their similarity in foraging behavior, we predicted that, if we were to find evidence of negative associations between natives and exotics, we would find them within

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**Fig. 2.** Native species richness as a function of non-native abundance in coastal sage scrub (CSS) at Camp Pendleton and Miramar, San Diego County, California ($n = 60$ sites).

**Fig. 3.** Detrended correspondence analysis (DCA) of native spider assemblages in coastal sage scrub (CSS) at Camp Pendleton and Miramar, San Diego County, California. Sites are labeled by non-native spider abundance, with L = 0–14 non-natives, M = 15–74, H = 75–148 (axis 1 gradient length = 2.8, $n = 60$ sites). Axis labels were determined by the highest correlation(s) between DCA scores for axes I and II and environmental variables.

**Fig. 4.** (A) Total spider abundance and (B) relative abundance of non-natives in coastal sage scrub (CSS) at Pendleton and Miramar, San Diego County, California, as related to distance from coast ($n = 60$ sites).
Table 1
Chi-squared test of improvement in a logistic regression model for proportion of native spiders at sites using seven environmental parameters with non-native species occurrence included (n = 60 sites; k = 7 environmental variables)

<table>
<thead>
<tr>
<th>Model</th>
<th>$-2 \log L$</th>
<th>$R^2$</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environment</td>
<td>291.477</td>
<td>0.58</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Environment + Trachyzelotes spp.</td>
<td>290.782</td>
<td>0.58</td>
<td>0.695</td>
<td>n.s.</td>
</tr>
<tr>
<td>Environment + Urozelotes rusticus</td>
<td>289.642</td>
<td>0.60</td>
<td>1.835</td>
<td>n.s.</td>
</tr>
<tr>
<td>Environment + Zelotes nilicola</td>
<td>290.366</td>
<td>0.58</td>
<td>1.111</td>
<td>n.s.</td>
</tr>
<tr>
<td>Environment + Dysdera crocata</td>
<td>286.252</td>
<td>0.61</td>
<td>5.225</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Environment + Oecobius annulipes</td>
<td>250.826</td>
<td>0.79</td>
<td>40.651</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

*a* n.s., not significant

4. Discussion

4.1. Documented interactions between non-native spiders and natives

Non-native spiders appear to affect natives more strongly in simpler, less productive urban landscapes than in natural ecosystems. In the eastern United States, the European theridiid *Steatoda bipunctata* appears to be displacing the native *Steatoda borealis* along urban interfaces (Nyffeler et al., 1986). In urban areas of southern California, the introduced marbled cellar spider (*Pholcidae: Holocnemus pluchei*) may be displacing the native black widow (*Theridiidae: Latrodectus hesperus*; W. R. Ice-nogle personal communication). In this study, non-native spiders were abundant in CSS and, at some sites, were numerically dominant, particularly in lowland, coastal sites (Fig. 4). Despite their prevalence, we failed to find a pattern that suggested non-native spiders were depressing native populations. There was a relationship between exotic and native spiders, but interestingly this association was positive, in that non-natives occurred where native spiders were both most abundant and most diverse.

4.2. Potential causes of observed patterns

Although we have no record of the spider fauna of CSS before the introduction of non-natives, we observed only positive associations between native and non-native spiders. Large-scale negative changes to a native arthropod fauna after the introduction of a non-native predator can and have occurred. For example, the non-native predator *Vespula vulgaris* (*Hymenoptera: Vespidae*) appears to be reducing densities of native spiders and insects (Harris and Oliver 1993), and in manipulative studies it has been found to significantly reduce numbers of orb weaver spiders (*Araneae: Araneidae*) (Toft and Rees, 1998).

The absence of a negative association between natives and non-natives in our study may be the result of several factors. Spider prey availability may be so high in the coastal region of San Diego County that competition for food between and predation from other spiders are relatively low. Examples of reduced competition due to high resource availability exist. Non-native predacious carabid beetles colonize sites quickly but do not reduce native congener density (Niemalä et al. 1997). Similarly, the introduced *Coccinella septempunctata* (*Coleoptera: Coccinellidae*) severely lowers survival of the related native *Coleomegilla maculata* at low prey density, but has no effect on the native species at high prey density (Obrycki et al. 1998).

Spider activity and/or abundance typically increase in relation to arthropod prey availability (Nentwig, 1982). Many spiders, being opportunistic hunters, utilize other spiders as prey (Polis et al., 1989, Wise, 1993). Adding species to a resource-rich environment could theoretically facilitate higher overall abundance and richness of species (*sensu* Hector et al., 1999). The positive association that abundance of both *Dysdera crocata* and *Oecobius annulipes* had with the proportion of natives independent of their association with environment (Table 1) may reflect such facilitation.

Table 2
Pearson product-moment correlations between gnaphosid spider species

<table>
<thead>
<tr>
<th></th>
<th>Drassyllus saphes</th>
<th>Drassyllus lamprus</th>
<th>Micaria icenoglei</th>
<th>Micaria utahna</th>
<th>Nodocion eclecticus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drassyllus fractus</td>
<td>0.43</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Haplodrassus signifer</td>
<td>n.s.</td>
<td>0.44</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Sergiolius angustus</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.43</td>
<td>n.s.</td>
</tr>
<tr>
<td>Urozelotes rusticus</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>0.61</td>
<td>n.s.</td>
</tr>
<tr>
<td>Zelotes nilicola</td>
<td>n.s.</td>
<td>0.66</td>
<td>n.s.</td>
<td>0.55</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

*a* All correlation coefficients presented were significant at $\alpha = 0.001$. The species *Urozelotes rusticus* and *Zelotes nilicola* are non-natives.

*b* n.s., not significant.
Spider assemblages may also have already changed in response to non-natives. We have no information as to the exact time of local invasion, the character of the cursorial spider community before invasion, or the current stability of assemblages. However, we have been unable to detect any evidence of competitive exclusion or local extirpation across a gradient of non-native abundance. Our results support recent contentions suggesting that highly diverse communities are more likely than simple systems to support invading species (Levine and D’Antonio, 1999, Levine, 2000). Colonization by non-natives does not necessarily mean that native species, communities, or ecosystems are adversely affected. Productivity can increase with diversity when species act as facilitators for one another rather than competitors within a hypothetical finite niche space (Hector et al., 1999). Highly linked, diverse natural systems may actually be able to support the establishment of a few invading species while still withstanding their potential negative effects. For example, grass tussocks supporting a high diversity of native plant species contain more non-natives than those with low diversity (Levine, 2000).

4.3. Associations within the Gnaphosidae

Because the Gnaphosidae are numerically dominant in ground-dwelling spider assemblages of CSS and contain several non-native species (which are behaviorally and ecologically similar to natives), we predicted native members of the family would be more affected by predation and/or competition from exotic gnaphosids than would other spider taxa. However, the only significant relationships we detected between native and non-native gnaphosid species were positive (Table 2). In another study, we observed that the native Drassyllus insularis, despite being otherwise common along the coast, was absent at three coastal sites supporting the highest numbers of the non-native Urozelotes rusticus (Prentice et al., 1998), suggesting that competitive displacement of natives may occur in this system at very high densities of exotic gnaphosids. Nonetheless, at a regional scale (coastal southern California, USA) the pattern we found of association between native and exotic gnaphosids does not suggest that these exotic species currently are negatively affecting their native congeners or con familiairs.

5. Conclusion

Intraguild predation is common in spiders (Hallander, 1970, Nentwig, 1986, Polis et al. 1989). Additionally, competition can be strong for food resources, nest and retreat sites, and hunting territory (Gertsch and Reichert, 1976, Schaefer, 1978, Reichert, 1981). Coexistence of closely related species by means of resource partitioning and alloptoy has been documented for the wolf spiders Pardosa rambulosa and Pardosa tuoba (Lycosidae; Greenstone, 1980). In our study, mesic coastal sites may currently contain ample prey and substrate complexity such that potential negative interactions between generalist non-native and native predators are minimized. Whereas biological invasions have proved devastating in many systems (Enserink, 1999, Kaiser, 1999, Malakoff, 1999) and indeed have seriously affected southern Californian ecosystems (Eliason and Allen, 1997), we failed to detect a deleterious impact of non-native spider species upon their native counterparts. Although we lack data from a manipulative experiment, regardless of mechanisms involved, our data support the hypothesis that non-native species are more common in areas with high biodiversity (Levine and D’Antonio, 1999), and thus do not support the hypothesis that non-natives will more readily establish in areas with low biodiversity. Highly linked, diverse communities may be more resilient to the deleterious effects of non-natives (Levine, 2000). We see a need for the development of better predictive models (based on life history and ecology) of the impact, and control, of ever-more-common biological introductions.

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