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Regional patterns in the invasion success of *Cheiracanthium* spiders (Miturgidae) in vineyard ecosystems

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Abstract Invasions have often been linked to reduced biodiversity, but the role of non-native species in the decline of native species is ambiguous. In a 2003 survey of four California vineyard regions, exotic spiders (*Cheiracanthium* spp.) were more dominant in vineyards with lower spider species diversity and reduced spider abundance. There was no evidence for the role of species interactions in the invasion of *Cheiracanthium* spiders, however, as native spiders from the same feeding guild were most abundant in regions with high *Cheiracanthium* levels. Comparison with a survey conducted 10 years earlier indicated that the recent invader *C. mildei* simply represented an addition to the spider community, with no apparent change in proportions of the congener *C. inclusum*. Invasion success is discussed with respect to agricultural habitat, as results suggest that disturbed conditions in many vineyards may favor *Cheiracanthium* spp. and native wandering spiders while decreasing overall spider diversity.

Keywords Araneae · Miturgidae ·
Cheiracanthium · Invasive species ·
Interspecific competition · Habitat fragmentation

Introduction

Invasive species threaten biodiversity in managed and natural ecosystems worldwide (Mack et al. 2000; Kolar and Lodge 2001). Invasions may result in species displacement (Parker et al. 1999; Levine et al. 2003; Yurkonis et al. 2005), although evidence is often indirect and difficult to obtain (Didham et al. 2005). It is still unclear whether the majority of invasions cause declines in biodiversity through the suppression of native species. Just as invasive species may be “drivers” of ecological change, they may also be “passengers” of anthropogenic changes to ecosystems that negatively impact native species (MacDougall and Turkington 2005). Highly disturbed, species-poor habitats may be more vulnerable to invasion than undisturbed habitats with high species diversity (Stachowicz et al. 1999; Shea and Chesson 2002; Kennedy et al. 2002). Weaker competition in species-poor habitats, due to an absence of ecologically similar native species, may allow invaders to establish more easily (Levine and D’Antonio 1999; Tilman 1999; Von Holle and Simberloff 2004; Yurkonis et al. 2005), leading to a negative association between invaders and ecologically similar native species. Alternatively, if non-native and native species respond positively to the same ecological conditions, invasions may be more successful in habitats with higher species diversity (Levine 2000). Under this mechanism, a positive correlation between native and non-native species would be expected.

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Generalist arthropod predators include invasive species that are capable of affecting native species through a variety of direct and indirect pathways (Snyder and Evans 2006). The negative impacts of invasive ant species, for example, have been enormous (Holway et al. 2002). As generalist arthropod predators, spiders have the potential to affect native arthropod species; nevertheless, spiders have been largely overlooked as invasive species (but see Nyffeler et al. 1986; Hann 1990; Burger et al. 2001; Gruner 2005). Once established, invasive spiders may be viewed as either beneficial arthropods in agroecosystems, or as disruptive predators in native ecosystems. Documented displacements of native by invasive spider species are rare, although Hann (1990) reported an invasive web-building spider competed with and ultimately displaced an endemic web-building species in New Zealand.

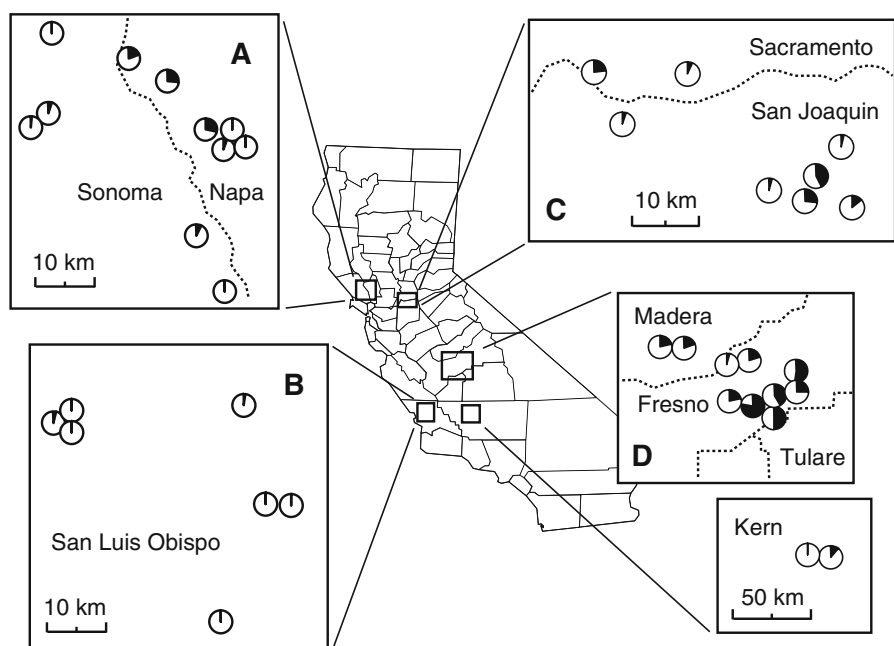
Here, we present results from surveys that documented exotic *Cheiracanthium* spiders (Miturgidae) in California vineyards. Spiders comprise most arthropod predators in California vineyards (Costello and Daane 1999) and surveys conducted in the 1990s found that among the wandering spider species was a yellow sac spider of the genus *Cheiracanthium* (Costello and Daane 1995, 1999). There are two known *Cheiracanthium* species in the Americas—*C. mildei* L. Koch, a Mediterranean native that was first

reported in New England in the late 1940s (Bryant 1952), and *C. inclusum* Hentz, which is present in Africa and the New World (Platnick 2008). Both are wandering nocturnal hunters that feed on a wide variety of prey (Peck and Whitcomb 1970; Mansour et al. 1980; Wise 1993). We predicted that the invasion success of *Cheiracanthium* spiders would be negatively correlated with the species richness and abundance of native spiders. In particular, we expected a negative association between *Cheiracanthium* spiders and ecologically similar native species (i.e., native wandering spiders).

Materials and Methods

Spider composition was surveyed in four major California vineyard regions in June and July 2003 (Fig. 1). The sampling period was selected to match the seasonal period when most vineyard spiders are adults or large immatures (Costello and Daane 1999), in order to facilitate species identification. Thirty-eight vineyard blocks were each sampled once: seven Central Coast wine grapes (San Luis Obispo County); eleven North Coast wine grapes (Napa and Sonoma Counties); twelve San Joaquin Valley raisin or table grapes (Madera, Fresno, and Kern Counties); and eight Northern Interior wine grapes (San Joaquin and

Fig. 1 Proportions of exotic *Cheiracanthium* spp. (black section of pie chart) and native spiders collected in 2003. Samples sites were within four California vineyard regions: **a** North Coast (Napa and Sonoma Counties); **b** Central Coast (San Luis Obispo County); **c** Northern Interior (San Joaquin and Sacramento Counties); **d** San Joaquin Valley (Madera, Fresno and Kern Counties)



Sacramento Counties). To examine the occurrence of *Cheiracanthium* spiders in vineyards outside California, five additional wine grape vineyards were sampled in northwestern Oregon (Benton County) in October 2006.

As was typical of the regional patterns of land use, Central Coast vineyards were surrounded primarily by oak woodland, while Northern Interior and San Joaquin Valley vineyards were surrounded by other agricultural blocks (vineyards and/or stone fruit orchards). Surrounding habitat in the North Coast region included other vineyards, oak woodland and grasslands. Oregon vineyards were surrounded by other vineyards or pine forests.

Spiders were sampled using a “beat” sampling method, as described by Costello and Daane (1997). Foliage between grape vines was shaken and beaten over a 1 m² cloth funnel for 30 s; spiders fell into a plastic bag attached with binder clips to the bottom of the funnel. In the field, collected samples were immediately deposited into a cooler to discourage spider-spider predation. Eighteen samples were taken from each site. Samples were collected from six vineyard rows; sampled rows were five rows apart, and three samples were taken per row at intervals of ten vines. All samples were sorted in the laboratory; spiders were deposited in 70% alcohol and identified using keys developed by Roth (1993) or Ubick et al. (2005). Most spiders were identified to species or genus. Immatures from some families (e.g., Araneidae, Linyphiidae) could not be sorted beyond the family level; these spiders were instead sorted to morphospecies.

To assess changes over time in *Cheiracanthium* abundance, samples from four vineyards in the 2003 survey were compared with samples collected from the same four vineyards in a 1993 survey (Costello and Daane 1995). The beat collection method was used in both surveys, and samples were taken during the same month in both years (June). The presence of *C. mildei* was not reported in these earlier surveys. To exclude the possibility that *C. mildei* had been overlooked, voucher specimens from 1993 surveys were examined to confirm species identity.

Data analyses

Differences between California regions in proportions of *Cheiracanthium* and native wandering spiders, species richness, and total spider abundance

were compared using Kruskal–Wallis tests. Nonparametric multiple comparison tests were performed using the `kruskalmc` function in R version 2.7.0 (R Development Core Team 2008). To examine spider community structure in vineyards, spiders were assigned to guilds following classifications in Uetz et al. (1999), with the exception of the “diurnal stalker” guild, which we refer to here as “jumping spiders” (Salticidae), since these were the only spiders representing this guild in our samples. Guild structure was compared between regions using the Bray–Curtis similarity index.

We used regression analysis to assess relationships between dominance of *Cheiracanthium* spiders (expressed as proportion of *Cheiracanthium* to total spiders) and species richness and total spider abundance. Data for California and Oregon were analyzed separately. It should be noted that species richness is necessarily correlated with abundance. We were unable to rarefy species richness, however, since the minimum number of spiders per vineyard was low ($n = 6$) and rarefaction curves tend to converge at low abundances (Gotelli and Colwell 2001). Nonetheless, we feel that the number of species present may be a useful ecological measure in itself. All vineyards where *Cheiracanthium* was not present ($n = 10$) were excluded from these analyses. Proportional data were arcsine square-root transformed (Systat 2007). Total spider abundance was log-transformed to meet assumptions of normality. For analyses of California data, region and insecticide use (high-input/low-input) were initially included as dichotomous dummy variables, but were insignificant at $P < 0.05$ and the data are not included here. Spearman rank correlation was used to assess the association between abundances of *Cheiracanthium* spp. and native wandering spiders across California sites, with the `cor.test` function in R.

To assess whether invasion levels of *Cheiracanthium* spiders changed between 1993 and 2003, proportions of *C. inclusum* and both *Cheiracanthium* spiders together were compared between years using Mann–Whitney tests.

Results

A total of 1367 spiders were collected from California vineyards, belonging to 17 families and 30

species (Table 1). *Cheiracanthium* spiders occurred at 28 out of the 38 vineyards sampled and comprised more than 25% of the spider composition at eight vineyards (Fig. 1). *Cheiracanthium mildei* and *C. inclusum* accounted for 4.2 and 2.6% of spiders overall. Native wandering spiders included three species: *Anyphaena pacifica* Banks, *Hibana incurva* Chamberlin (both Anyphaenidae) and *Trachelas pacificus* Chamberlin (Corinnidae). The majority of identified species were restricted to North America (Platnick 2008) and are, therefore, likely to be native. Only five of the species collected show a wider distribution: *Salticus scenicus* Clerck (Salticidae) and *Misumena vatia* Clerck (Thomisidae), which are Holarctic; *Badumna longinqua* L. Koch (Desidae), which is present in Australia, New Zealand and the New World, but was represented by only one individual in our surveys; and the two *Cheiracanthium* species, *C. mildei* and *C. inclusum*. Of these, only *B. longinqua* and *C. mildei* are known to be exotic, while the presence of *C. inclusum* in Africa and the New World (Platnick 2008) strongly suggests that it is also an invader to North America (*Cheiracanthium* is primarily an Old World genus; *C. mildei* and *C. inclusum* are the only *Cheiracanthium* species known to be present in the Americas).

There was wide variation among the 38 vineyards in total number of spiders collected (range: 6–146) and number of spider species per vineyard (range: 4–20). There were also stark differences in the spiders that dominated each vineyard region (Fig. 2). The only spider guild that was consistently represented in all regions was the jumping spiders (Salticidae). Funnel weavers, orb weavers, and diurnal wandering spiders were not represented in most vineyards. According to the Bray-Curtis index, North Coast and Northern Interior vineyards showed the greatest similarity in guild structure of all regions within California (Table 2). Spider guild composition in the San Joaquin Valley was not similar to any other region, and was most dissimilar to the Central Coast (Table 2). Guild structure and species composition of Oregon vineyards was very similar to North Coast vineyards (Table 2). *Cheiracanthium* spiders were present in all vineyards sampled in Oregon.

Regional differences in species richness within California were only marginally significant (Kruskal–Wallis test, $H = 6.82$, $P = 0.078$), although the Central Coast had the highest number of species per

vineyard, while the San Joaquin Valley had the lowest (Fig. 3). There were significant differences between regions in total numbers of spiders per vineyard ($H = 9.71$, $P = 0.02$), percentages of *Cheiracanthium* spiders ($H = 15.78$, $P < 0.01$) and percentages of native wandering spiders ($H = 14.42$, $P < 0.01$). Vineyards in the San Joaquin region contained the lowest numbers of spiders and spider species of all regions within California, the highest proportions of *Cheiracanthium* spiders and native wandering spiders (Fig. 3). The Central Coast, in contrast, showed the highest numbers of spiders and spider species, but had the lowest numbers of both *Cheiracanthium* spiders and native wandering spiders.

Across California, there were significant negative relationships between proportion of *Cheiracanthium* spiders and both total number of spiders per vineyard and species richness (Fig. 4). Vineyards with low spider abundance and low species richness tended to have higher proportions of *Cheiracanthium* spiders. There was a marginally positive correlation, however, between *Cheiracanthium* spiders and native wandering spiders (Spearman rank correlation, $r = 0.30$, $P = 0.07$).

There was also a marginally significant negative relationship between proportion of *Cheiracanthium* spiders and total spider numbers per vineyard in Oregon ($R^2 = 0.75$, $P = 0.058$; arcsine $\sqrt{\text{proportion } Cheiracanthium} = 1.42 - 0.66 * \log(\text{spider number})$), while the relationship between proportion *Cheiracanthium* and species richness was negative but nonsignificant ($R^2 = 0.49$, $P = 0.19$; arcsine $\sqrt{\text{proportion } Cheiracanthium} = 0.73 - 0.03 * \text{number species}$).

In comparisons of San Joaquin Valley samples from 1993 and 2003, a striking change in species incidence and proportional representation occurred within the *Cheiracanthium* spiders. *C. mildei* was not represented in samples from 1992 to 1993, but was the dominant *Cheiracanthium* species in 2003. In our reexamination of voucher specimens from 1992 to 1993, all *Cheiracanthium* spiders were confirmed to be *C. inclusum*, as reported by Costello and Daane (1995). Percentages of *Cheiracanthium* spiders in 1993 and 2003 were 15.8 ± 5.1 and 57.1 ± 12.0 (means \pm SE), respectively, and were significantly higher in 2003 (Mann–Whitney test, $P < 0.05$). Percentages of *C. inclusum* were 15.8 ± 5.1 in 1993 and 19.3 ± 13.5 in 2003, and were not significantly different between years ($P > 0.05$).

Table 1 Total numbers of spiders collected in 2003 (California) and 2006 (Oregon)

Spider	Total numbers of spiders by region				
	San Joaquin Valley	Northern Interior	North Coast	Central Coast	Oregon
Agelenidae					
<i>Hololena nedra</i>	17	6	0	0	0
Anyphaenidae					
<i>Anyphaena pacifica</i>	1	2	31	1	9
<i>Hibana incursa</i>	2	0	0	0	0
Araneidae					
<i>Cyclosa</i> sp.	0	0	1	1	1
<i>Neoscona</i> sp.	2	0	0	0	0
<i>Nuctenea</i> sp.	0	0	3	0	0
Unidentified araneids	2	4	7	3	0
Clubionidae					
<i>Clubiona</i> sp.	0	0	0	0	1
Corinnidae					
<i>Trachelas pacificus</i>	58	1	20	1	0
Desidae					
<i>Badumna longinqua</i>	0	0	1	0	0
Dictynidae					
<i>Dictyna</i> sp.	2	6	63	7	6
Gnaphosidae					
Unidentified gnaphosids	6	3	6	2	3
Linyphiiniidae					
Erigoninae (dwarf spiders)	5	71	37	5	19
Unidentified linyphiids	1	0	12	7	2
Lycosidae					
Unidentified spp.	0	2	2	1	0
Miturgidae					
<i>Cheiracanthium mildei</i>	42	7	8	1	16
<i>Cheiracanthium inclusum</i>	17	12	7	0	1
<i>C. mildei</i> or <i>C. inclusum</i>	4	4	4	2	0
Oxyopidae					
<i>Oxyopes salticus</i>	2	1	72	1	0
<i>Oxyopes scalaris</i>	21	0	5	4	24
<i>Oxyopes</i> sp.	0	5	3	0	1
Philodromidae					
<i>Ebo</i> spp.	0	0	3	30	3
<i>Philodromus</i> spp.	0	0	1	0	20
<i>Tibellus</i> sp.	0	0	1	0	6
Salticidae					
<i>Metaphidippus manni</i>	4	1	20	33	150
<i>Phidippus</i> spp.	2	21	13	19	4
<i>Sassacus vitis</i>	36	0	0	0	8
<i>Salticus scenicus</i>	0	2	41	3	4
Unidentified salticids	11	4	17	18	1

Table 1 continued

Spider	Total numbers of spiders by region				
	San Joaquin Valley	Northern Interior	North Coast	Central Coast	Oregon
Tetragnathidae					
<i>Tetragnatha laboriosa</i>	0	1	16	2	1
Theridiidae					
<i>Theridion</i> spp.	4	23	14	6	7
Unidentified theridiids	0	0	0	0	6
Thomisidae					
<i>Coriarachne brunneipes</i>	1	13	2	0	1
<i>Misumena vatia</i>	0	0	0	6	4
<i>Misumenops</i> sp.	0	1	2	11	13
<i>Xysticus gulosus</i>	3	4	35	303	
Unidentified spiders	7	1	5	3	0
Total spiders	250	195	452	470	312

Fig. 2 Regional comparison of spider guild composition in California vineyards. Data are mean percentages of each guild for each region

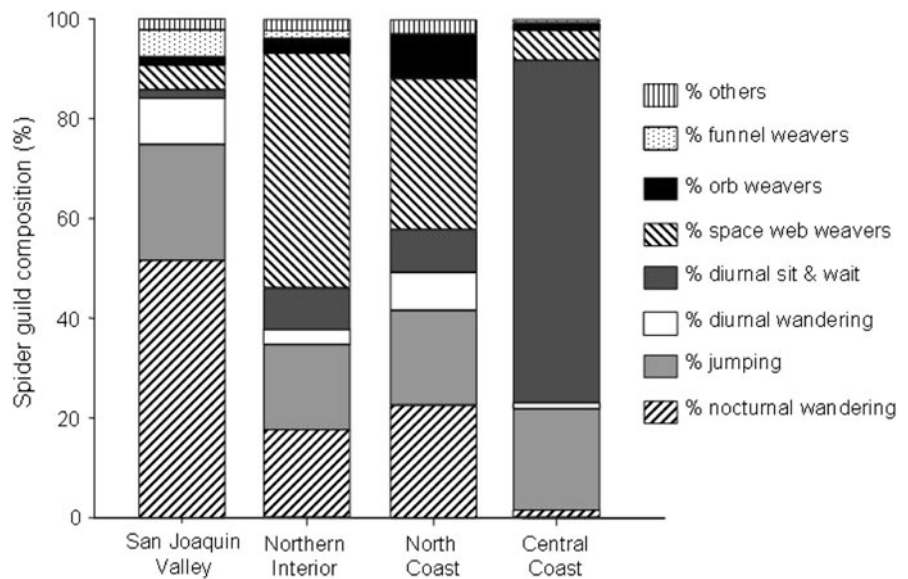


Table 2 Comparisons of spider guild composition between regions using the Bray-Curtis similarity index. Samples were pooled for each region; mean number of spiders in each guild for each region was used in calculating the index

	North Coast	Central Coast	Northern Interior	San Joaquin Valley	Oregon
North Coast	–	–	–	–	–
Central Coast	0.34	–	–	–	–
Northern Interior	0.69	0.26	–	–	–
San Joaquin Valley	0.48	0.18	0.46	–	–
Oregon	0.61	0.39	0.44	0.34	–

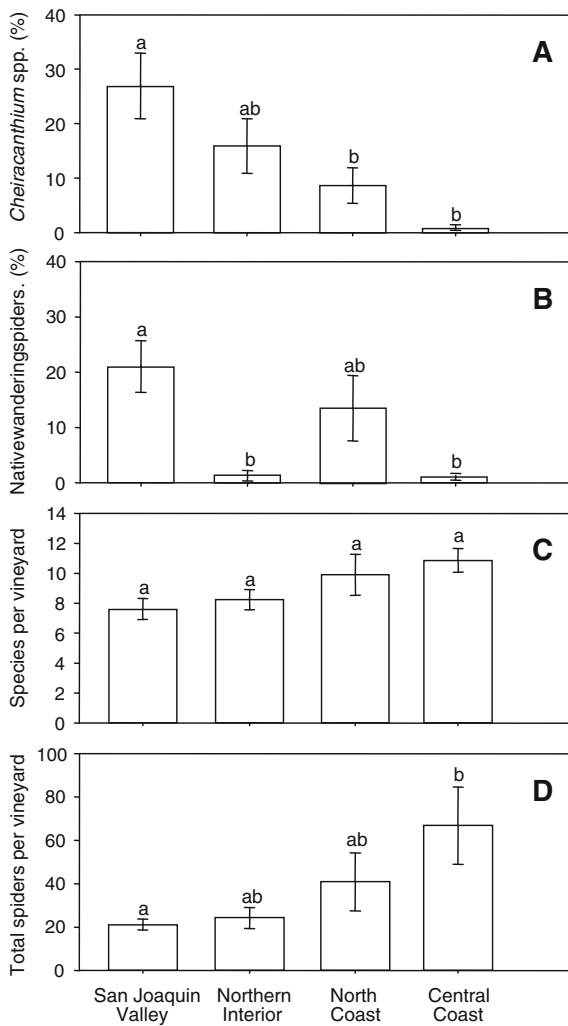


Fig. 3 Influence of four different grape-growing regions on **a** percentage of *Cheiracanthium* spiders, **b** percentage of native wandering spiders, **c** species richness, and **d** total number of spiders. Data are means \pm SE. Different letters above means indicate that they are significantly different (nonparametric multiple comparison tests, $P < 0.05$)

Discussion

In California, *Cheiracanthium* spiders appeared to have been most successful in vineyards where abundance and diversity of native species was depleted. To examine the consistency of this pattern, we also sampled vineyards outside California, and showed that a similar, marginally significant relationship between proportions of *Cheiracanthium* spiders and total spider abundance was present in Oregon. The role of species interactions in the

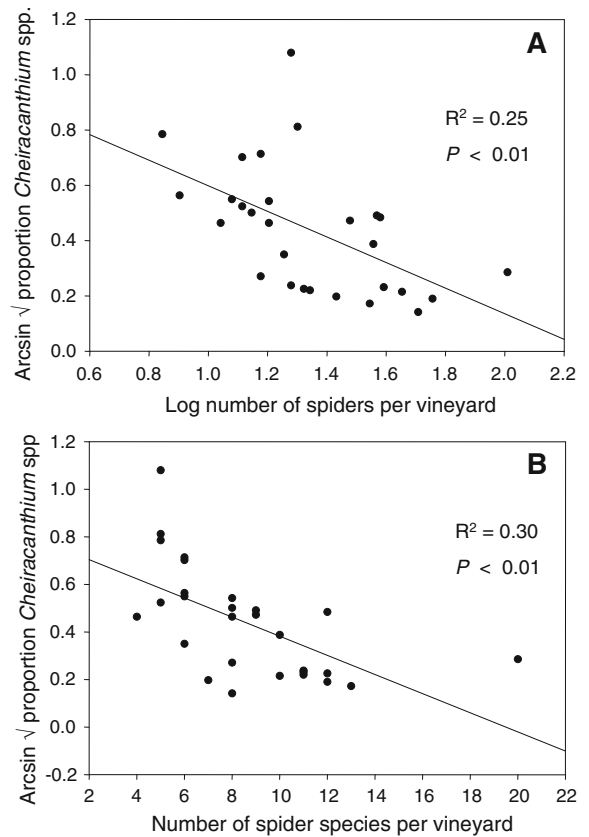


Fig. 4 Relationship between the proportion *Cheiracanthium* spiders of total spiders (arcsine square-root transformed) in each vineyard with **a** the total number of spiders (\log_{10} -transformed) and **b** the number of spider species in each respective vineyard. Data are from 2003 collections; vineyards where *Cheiracanthium* spiders were not present were excluded from analyses

invasion of *Cheiracanthium* spiders was ambiguous, however. *Cheiracanthium* spiders were most successful in California regions where native wandering spiders were also abundant, and there was even a marginally positive correlation between abundances of *Cheiracanthium* and native wandering spiders. The comparison of spider species composition in San Joaquin Valley vineyards between 1993 and 2003 also yielded little evidence for species interactions in the invasion of *Cheiracanthium* spiders. Although invaders are likely to interact most strongly with ecologically similar native species (Prieur-Richard et al. 2000; Symstad 2000), the presence of both *Cheiracanthium* species in many of the same vineyards in 2003 suggests that these species may coexist in vineyards. The large increase in the proportion of

Cheiracanthium spiders between years appears to be due to the addition of *C. mildei* to the spider fauna.

This pattern runs contrary to the view that invasive species should be more successful in ecosystems where functionally similar native species are absent (e.g., Von Holle and Simberloff 2004). Other studies examining invasions of generalist arthropod predators have uncovered similar results. An invasive carabid beetle, for example, appeared to coexist with native carabids (Niemelä and Spence 1991; Niemelä et al. 1997). Similarly, Burger et al. (2001) found a positive correlation between numbers of exotic spiders and native spiders, and concluded that non-native spiders represented a supplement to native spider diversity. High prey availability may prevent predator-predator competition from occurring, as seemed to be the case with a non-native coccinellid beetle, which suppressed a native coccinellid at low prey densities but not at high prey densities (Obrycki et al. 1998). The setting of this study may also have precluded species interactions; long-term dynamics may not be possible in agricultural systems, due to disturbance from insecticide applications and other farming practices (Janssen et al. 2006). The roles of short- and long-term dynamics in the relatively recent arrival of *C. mildei* are also difficult to determine, as *C. mildei* has either been present in these sites for less than 10 years, or has not become established over the long-term, and has repeatedly recolonized vineyards after dispersal events or population declines.

Notwithstanding these considerations, regional dominance of *Cheiracanthium* spiders appears to have scaled negatively with increased prominence of natural habitat in the landscape (San Joaquin Valley > Northern Interior > North Coast > Central Coast), while total spider abundance and spider diversity showed an opposing pattern. High percentages of non-crop habitats surrounding crop systems can influence spider composition (Schmidt and Tscharrntke 2005) and diversity (Clough et al. 2005). Here, we did not directly measure the amount of non-crop habitat in each region, but we suspect that the complexity of the surrounding landscape may be important in explaining regional patterns in both spider diversity and the invasion success of *Cheiracanthium* spiders. It should be noted that we are unable to rule out the influence of other factors that could have contributed to observed patterns, such as propagule pressure, which may influence the

success of invasions more than characteristics of invaded communities (Levine 2000; Von Holle and Simberloff 2005), or possible differences between regions in numbers of spider predators such as birds, which Gruner (2005) showed could profoundly influence the success of spider invasions.

However, the negative relationships between proportions of *Cheiracanthium* spiders and both numbers of spiders and species richness are likely to reflect the adaptability of *Cheiracanthium* spiders, as was noted by Costello and Daane (1995). Invasive species may be passengers of large-scale changes in environmental conditions that negatively affect native species (Shea and Chesson 2002; MacDougall and Turkington 2005), and the conversion of landscapes to vineyard monoculture may allow *Cheiracanthium* spiders to thrive at the expense of native spider diversity. Vineyard monoculture may not be a hostile environment for native wandering spiders, however. The co-occurrence of *Cheiracanthium* spiders with native wandering spiders may reflect similar responses to disturbance. The adaptability of *Cheiracanthium* spiders may not result solely from their status as exotic species, but may be characteristic of wandering spiders in general. Non-native and native species can respond positively to the same environmental conditions (Levine 2000; Burger et al. 2001), and the wandering spider guild as a whole may flourish under conditions that are hostile to other spider species.

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