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Influence of invasive palms on terrestrial arthropod assemblages in desert spring habitat

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ABSTRACT

Invasive plants can eliminate native flora and ultimately have negative indirect effects on fauna and the functional ecology of ecosystems, but understanding of these cascading effects on arthropod assemblages is poor. Desert spring habitats are small, isolated landscape elements that are literal oases for flora and fauna and support high diversity assemblages; invasive palms can colonize desert springs and form monocultures. In an effort to understand effects of these invasive trees on higher terrestrial trophic levels at springs, we contrasted assemblage structure of terrestrial arthropods in native vegetation versus invasive palm habitat. We sampled arthropods in paired palm and native habitat at ten springs in Death Valley National Park, California, USA, during both spring and fall growing seasons using suction sampling. Invading palms supported a mean of only one-sixth of the arthropod abundance, one-third of the species richness, and half the family richness of native habitat. Almost all orders were less abundant in palms, and most families and species were either absent or virtually absent in palm habitat. Both live and dead palm leaves were depauperate, and season and block effects were minimal. Impacts of these visually striking invasives clearly go beyond monopolization of ground cover, and invading palms appear capable of reshaping the functional ecology of desert springs. If control efforts are undertaken, we recommend complete removal of palms, because killed but standing "ghost palms" and associated thatch persist for many years and will continue to provide poor arthropod habitat and prevent native plant establishment.

Keywords: desert springs, invasive palms, isolated habitats, indirect effects, shrubland, terrestrial arthropod assemblage

1. INTRODUCTION

Invasive vegetation can outcompete native flora and ultimately have negative indirect effects on fauna and the functional ecology of ecosystems (Williams and Karl, 2002; Samways, 2005; Traveset and Richardson, 2006), but there is relatively poor understanding of these cascading effects on arthropod assemblages (Samways, 2005). Woody invasive plants may have a particularly deleterious effect on native arthropod assemblages (Samways, 1994; Samways et al., 1996), and this effect may be pronounced when a woody invader overstory replaces a complex vertical structure previously composed of native shrubs, grasses, and forbs (Bieringer and Zulka, 2003; Samways and Taylor, 2004; Smith et al., 2007) or when such invasion occurs in habitats with limited spatial extent (Samways et al., 2005; Smith et al., 2007; Remsburg et al., 2008). Insect trophic complexity (Olckers and Hulley, 1991; Samways et al., 1996), growth rate (Chown and Block, 1997), and biomass (Tallamy, 2004) can also be reduced among alien plants.

It is not a given, however, that invasive vegetation will degrade associated arthropod assemblages (Samways, 2005). Samways and Sharatt (2010) found lower abundances of dragonflies associated with invasive trees but similar species richness relative to native plants. There may be taxon specific responses to increases in invasive vegetation, with some faunal taxa increasing and others decreasing (Samways et al., 1996), and generalist arthropod taxa are most likely to exploit invasive plants (Samways, 2005). Further, response of the terrestrial arthropod assemblage may be dependent on the nature of the invasive vegetation; Samways and Moore (1991) reported a decrease in grasshopper species richness and diversity under introduced pines but an increase in species richness and abundance under introduced cypress.

Desert springs are small, isolated landscape elements (Leibowitz, 2003; Leibowitz and Nadeau, 2003; Tiner, 2003) that are surrounded by an inhospitable matrix and are often characterized by relatively short vegetation such as shrubs and grasses (Stevens and Meretsky, 2008). These springs are high diversity oases for both plants and animals (Harris, 1992; Shepard, 1993; Kodric-Brown et al., 2007) and are disproportionately important to regional ecology (Stevens and Meretsky, 2008). Most research assessing influences on diversity and abundance of desert spring fauna has focused on vertebrates (Szaro and Jakle, 1985; Bradford et al., 2003; Kodric-Brown et al., 2007; Kodric-Brown and Brown, 2007) and aquatic invertebrates (Myers and Resh, 1999; Myers et al., 2001; Sada et al., 2005; Blinn, 2008); the diverse terrestrial invertebrate assemblage has received much less attention (Perla and Stevens, 2008; see also Stevens and Bailowitz, 2008; Crews and Stevens, 2009).

Palms can invade and proliferate in desert springs that lack native palms and that have historically been dominated by shrubs and other vegetation (Cornett, 1987, 2008, 2010; Loope et al., 1988; Kodric-Brown et al., 2007; Unmack and Minckley, 2008). Rapidly growing palms outcompete other plants via interactions with water, light, and fire, and their dense root masses, wide frond skirts, and fallen fronds inhibit establishment by other plants (Vogl and McHargue, 1966; Cornett, 1985, 2008, 2010; Kelly, 2007; Unmack and Minckley, 2008).

Does palm invasion of isolated desert springs result in a different terrestrial arthropod assemblage relative to that supported by eliminated native vegetation? Fauna may be diverse and abundant in native shrubland vegetation at these oases, but palms may degrade arthropod assemblages via shading and reduction of structural complexity and taxonomic diversity of desert spring flora. We compared terrestrial arthropod assemblages in palm and native habitat at replicate springs, each of which had both palms and native vegetation present. We repeated this paired sampling in both spring and fall growing seasons to determine if any relationships shifted as a function of season in the severe desert environment.

2. METHODS

The paired comparison of arthropod assemblages in palm and native habitat used individual desert springs in Death Valley National Park (California, USA) as blocks, and spring and fall sampling efforts were repeated measures. Generalization from responses of selected arthropod taxa can be misleading (Gibson et al., 1992), so we examined effects across all vegetation associated arthropod taxa that were collected by vacuuming.

2.1. Study area and sites

Death Valley National Park is located in the Mohave Desert of southeastern California, USA, near the Nevada border, ~160 km west of Las Vegas, Nevada. The floor of Death Valley (-85 masl at lowest point) is one of the most extreme environments in the world; mean rainfall is 4.2 cm per year, most of which falls between November and March, and the average daily maximum July temperature is 47^{o}C, with a record of 57^{o}C (Björkman et al., 1972: Loope et al., 1988). The primary growing season is in spring, following winter precipitation (January-March $\bar{x}$= 3.0 cm) and with accompanying warming temperatures; there is often a secondary pulse of growth for some plants in the late fall, as some new winter precipitation falls (September-November $\bar{x}$= 0.44 cm) and before temperatures become too cold. We sampled all sites in March, and again in November, of 2009.

The native vegetation of Death Valley springs is dominated by shrubs (Cornett, 1987, 2010), but springs have been invaded by two species of palms: the exotic date palm *Phoenix* *dactylifera* L. (Loope et al., 1988; Shepard, 1993; Cornett, 2010), and the California fan palm *Washingtonia filifera* (Linden ex André) H. Wendlo., which is native to southern California but only recently naturalized to the north in Death Valley (Cornett, 1987, 2008, 2010; Loope et al., 1988). Date and fan palms are both Arecaceae, with similar large, waxy, and fibrous leaves and generally unbranched trunks (Hickman, 1993). The Park is attempting to control both palm species; there have also been palm control efforts in other desert spring/riparian environments (Kelly, 2007; Kodric-Brown et al., 2007).

We sampled ten spring sites that had some of the most extensive palm invasion in the Park. Sites were dispersed along 80 km of the floor of Death Valley and the western slopes of the Grapevine and Funeral Mountains; site elevation ranged from -39 to 999 masl ($\bar{x}$= 410, SE= 132). We thus used a relatively large number of blocks over a broad landscape with good replicate dispersion (Hurlbert, 1984). The specific sites were Furnace Creek, North Travertine Springs, South Travertine Springs, Texas Springs, Cow Creek, Nevares Springs, Grapevine Canyon, Scotty's Castle, North Grapevine Springs, and South Grapevine Springs; all were spring sites regardless of place name. Cornett (1987, 2010) documents several of these sites in text and photographs. Palms are apparent in Cornett's images, though populations have since expanded at several sites, especially in the Travertine Springs complex. Spring area was determined for each site using aerial images from the US National Agriculture Imagery Program in ArcGIS 9.3.1. We calculated palm-occupied area by determining the percentage of points in a 10 m grid layer that overlaid palm habitat.

Plant species composition and richness for spring sites were derived from Death Valley National Park records and direct observation while sampling. Common shrubland taxa at our spring sites included: arrowweed *Pluchea sericea* (Nutt.) Coville, desert baccharis *Baccharis* *sergiloides* A. Gray, desert holly *Atriplex hymenelytra* (Torr.) S. Watson, cattle saltbush *A. polycarpa* (Torr.) S. Watson, saltgrass *Distichlis spicata* (L.) E. Greene, Nevada goldenrod *Solidago spectabilis* (D. C. Eaton) A. Gray var. *confinis* (A. Gray) Cronquist, western honey mesquite *Prosopis glandulosa* Torr. var. *torreyana* (L. D. Benson) M.C. Johnst., Arizona honeysweet *Tidestromia oblongifolia* (S. Watson) Standl., California loosestrife *Lythrum californicum* Torr. & A. Gray, and Mojave seablite *Suaeda moquinii* (Torr.) Greene.

2.2. Field and Lab Methodology

At each site, we randomly located two palm subsampling locations. An associated native vegetation subsample was located 5 m away from each palm habitat subsample in a randomly selected direction. Palm subsamples fell in date palm habitat at two sites, and the rest were in the more common fan palms. The same subsample locations were used for both March and November sampling.

The rigid branched nature of both the palm and native habitat precluded many collecting methods, and we used catch-per-unit-effort vacuum sampling, which has a record of successful application in studies of invertebrates in complex vegetation and can capture both volant and sedentary arthropods (e.g., Richmond and Graham, 1969; Macleod et al., 1994; Buffington and Redak, 1998). Vacuum sampling is an efficient technique for estimating abundance and species richness, relative to some other collecting methods (Arnold et al., 1973; Törmäla, 1982; Buffington and Redak, 1998), and also causes less damage to invertebrates than some other techniques (Callahan et al., 1966). Vacuum collection effort is consistent because of constant velocity, and the nozzle and suction can penetrate into the interior of a complex canopy (Buffington and Redak, 1998).

We used a Craftsman blower/vacuum, similar to the apparatus of Stewart and Wright

(1995), with an 11 cm aperture modified with a nylon 0.25mm square mesh collecting chamber inserted in the intake tube. Both Stewart and Wright's (1995) pitot tube measurements and our estimates with an anemometer indicate velocities well in excess of the minimum velocities required for successful extraction of arthropods from vegetation (Southwood, 1978). The nozzle of our vacuum was worked through the vegetation at each subsample location for 30 sec. A single operator did all of the vacuum sampling. All palm or native habitat at a given subsample location was sampled, whether leaves were alive or dead. Although shrubs dominated the native subsample locations, we sampled any native vegetation present at the subsample location. We did not sample the substrate in either habitat. After vacuuming, the integral mesh collecting bag was removed from the intake tube, and the fauna and associated plant debris were transferred to a re-sealable plastic bag, which was placed on ice and frozen as soon as possible (0.5 to 4 hours later). The two subsamples, from either palm or native habitat, were combined into a single one-minute catch-per-unit-effort sample/habitat type/replicate site.

We recorded some coarse physical and vegetation data for general habitat description. Air temperature (in shade) was recorded at each native-palm subsample location (i.e., two recordings/spring site/sampling visit) with a Kestrel 3000 digital meter. We measured percent canopy cover with a convex spherical densiometer (Lemmon, 1957; manufactured by Forest Densiometers) held at 100 cm above the substrate at each palm and each native subsample location in both spring and fall. After sampling palm habitat, we recorded the percent of sampled habitat represented by living leaves versus dead leaves for each palm subsample. Lastly, we estimated percent cover by common plant species at the native subsample locations.

Sorting of terrestrial fauna from plant debris was done in the laboratory, and we identified these small taxa (most < 2mm length) to as low a level as possible, usually to genus or species. Identification to species was not always possible due to an abundance of immature specimens and undescribed species and because a number of groups await revision. Vouchers were deposited with the National Park Service, University of California, Canadian National Collection (*Dasyhelea*, ceratopogonid midges), and Ohio State University (*Procaeculus*, caeculid rake-legged mites).

2.3. Analysis

We compared the influences of habitat type, site variability, and season on terrestrial arthropod assemblages with 1x2 blocked ANOVAs with repeated measures, supplemented by paired t-tests, linear regressions, and tests for trends across suites of metrics, using SYSTAT 12. Analyzed faunal metrics included order, family, and species population abundances and family and species richness. Collections with large numbers of individuals will have more species than collections with fewer individuals, even if drawn from equivalent sample sizes, so we also assessed richness with expected number of species after scaling to the number of individuals in the sample with the fewest individuals (i.e., expected number of species, $E(S_2)$; Hurlbert, 1971; Simberloff, 1972; Magurran, 2004). Such compensation for differing abundance via rarefaction is also useful because we were necessarily comparing results across different habitat configurations. We analyzed species dominance (Berger and Parker, 1970; May, 1975; Magurran, 2004) and probability of interspecific encounter (P.I.E.), i.e., the probability that two species drawn from a sample are of different taxa, as a measure of evenness (higher values indicate greater evenness; Hurlbert, 1971). We calculated $E(S_2)$ and P.I.E. using the application Diversity. Prior to field work, we used G*Power (Erdfelder et al., 1996; Faul et al., 2007; Mayr et al., 2007), our known sampling design and sample size, and the standard a priori estimate for effect size of 0.5 (Cohen, 1988; Lipsey and Wilson, 1993; Bausell and Li, 2002), to estimate power a priori rather than retrospectively (Hoenig and Heisy, 2001; Nakagawa and Foster, 2004). The planned ANOVAs had a power of 0.87 or better. Measures that demonstrated departures from normality via Lilliefors tests (Lilliefors, 1967) and/or had heterogeneity of variance ($F_{\max}$ and Cochran's tests; Cochran, 1941; Kirk, 1982) were successfully corrected with square-root transformations ($(y)^{0.5} + (y + 1)^{0.5}$) of proportional data and log transformations ($\log (y + 1)$) of all other data such that parametric assumptions were met. We used the sequential Bonferroni adjustment (Holm, 1979; Rice, 1989; Shaffer, 1995; Jaccard and Guilamo-Ramos, 2002) to calculate alternative, conservative probability values for contrasts within a given order such that the collective error rate was 0.05. Corrections were done with the application MacBonferroni. We calculated beta diversity (b_W-1; Whittaker, 1960; Magurran, 2004) and the Sørenson quantitative similarity index (Bray and Curtis, 1957; Faith et al., 1987; Clarke and Warwick, 2001; Magurran, 2004), which uses quantitative abundance data, to assess the relative diversity contributions of the native and palm assemblages. We also constructed rank abundance plots which provide an additional perspective on diversity, richness, and evenness, without the information losses associated with collapsing extensive assemblage information into a single number (Stiling, 2001; Magurran, 2004; Underwood and Fisher, 2006).

3. RESULTS

3.1. Vegetation and Physical

Springs ranged in size from 1.79 to 136 ha ($\bar{x}$= 39.7 ha, SE= 16.4), and the percentage of spring area occupied by palms ranged from 2.6 to 55% ($\bar{x}$= 17%, SE= 4.8). The native plant assemblage was relatively diverse with an average of 33.7 (SE= 5.7) species at each spring. *Pluchea* and *Baccharis* averaged 35.2% (SE= 11.5) and 12.5% (SE= 5.40), respectively, of the plant cover at the sampling sites. Each of the other taxa (see 2.1) accounted for less than 10% of the assemblage. Species richness of native plants was not related to spring area (p= 0.93, adjusted $R^2 < 0.00001$). Palms tended to invade wetter, more diverse sites; palm cover and species richness of native plants were positively correlated at the scale of total extent of each spring site (p= 0.0010, adjusted $R^2 = 0.73$). Canopy cover was higher in the palms ($\bar{x}$= 79.8%, SE= 8.7) than native shrubland ($\bar{x}$= 17.5%, SE= 7.4, p= 0.00016, ANOVA). Palm habitat was almost evenly divided between living ($\bar{x}$= 49.8%, SE= 12.4) and dead ($\bar{x}$= 50.2%, SE= 12.4) leaves (p= 0.91, 2-tailed t-test) when averaged across sites. Daytime air temperature was 23.7^{o}C (SE= 1.1) in March versus 19.5 (SE= 0.57) in November (p= 0.0059, one-tailed t-test).

3.2. Fauna

Invading palms supported a mean of only one-sixth of the arthropod abundance, one-third of the species richness, and half the family richness of native habitat, and these differences were all highly significant (Table 1). Probability of interspecific encounter was also significantly lower in palms than native vegetation (p= 0.0057, Table 1). Mean expected number of species was lower in palms, and mean percent dominance was higher, relative to shrubland; the associated p-values were low but not significant (p= 0.053 and 0.12, respectively, Table 1). Palms had a generally more depauperate fauna relative to native habitat across all assemblage metrics ($p= 0.00024$, one-tailed sign test). Palms also had a significantly lower percentage of herbivores than native habitat ($p= 0.029$, Table 1), which equated to a mean of only 1.1 herbivores per palm sample versus 16.5 herbivores per native sample. There were no significant differences for the other coarse feeding groups. Regressions of faunal metrics on species richness of native plants were not significant; e.g., relationships for total individuals and arthropod species richness yielded $p> 0.6$ and $R^2< 0.00001$ for each regression on plant species richness. In contrast to Habitat effects, there were no significant Season effects or Habitat x Season interactions for any of the assemblage or trophic group comparisons, and only one significant Block effect (total individuals, Table 1).

We collected arthropod fauna from 14 orders and 80 families in the study; only 39 of these families were found in the palms versus 67 in native habitat (see Supplementary material). Families were more evenly represented by season: 61 in spring and 50 in fall. There was a moderate level of beta diversity (0.51) across the two habitat types, and similarity was relatively low (0.21). Seventy percent of taxa present in palms were also found in native habitat; animals found exclusively in palms were not abundant. The rank abundance plots reflected the much smaller number of individuals and families in the palms, but the shape of the curves was similar and fell between log normal and broken stick configurations for both palm and native habitat (Fig. 1).

The most common orders across habitats and seasons were Diptera, Hemiptera, and Araneae, and eight of the ten most common families were from each of the first two orders, but there were a number of population differences between palm and native habitat at both the order and family levels (Table 2). Most testable comparisons indicated significantly higher order and family abundances in native vegetation versus palms. Some abundant families were completely absent from palms, including mirid plant bugs, which were a dominant herbivorous family in shrubland, and caeculid rake-legged mites. Other families that were important herbivore components of the native fauna, such as cicadellid leafhoppers and aphids, were almost absent from palms (Table 2). There was an overall trend of lower population abundances in palms relative to native habitat across all orders and the most abundant ten families ($p = 0.00008$, one-tailed sign test). The same held for comparisons across all 80 families; 63 families were less abundant in palms than in native vegetation ($p < 0.00001$, one-tailed sign test; see Supplementary material). Only one uncommon family, Anyphaenidae (Araneae), was much more abundant in palm than in native habitat (see Supplementary material), but this family was only twenty-third in overall abundance. The most abundant orders in native habitat were, in descending order, Diptera, Hemiptera, and Acari, versus Diptera, Araneae, and Hemiptera in palms (Table 2). Chironomid midges, cicadellid leafhoppers, and mirids were the most abundant families among native plants, versus chironomids, sciarid fungus gnats, and anyphaenid spiders in palms (Table 2; see Supplementary material).

Species data echoed the trends observed at the order and family levels. Most species had higher numbers in native habitat than in palms, as demonstrated by the most abundant taxa: *Empoasca cerea* DeLong (cicadellid, $\bar{x} = 4.0$ and 0.10 individuals per sample in native and palm habitat, respectively), *Melanotrichus/Parthenicus* group (mirid, 2.5, 0.0), *Dasyhelea* undescribed sp. cf. *ancora* (Coquillett) (ceratopogonid midge, 4.6, 0.30), *Tanytarsus* sp. (chironomid, 10.5, 1.3), *Limnophyes* sp. (chironomid, 3.7, 0.70), *Parametriocnemus* sp. (chironomid, 2.1, 0.30), *Sympycnus* undescribed sp. cf. *breviventris* Van Duzee (dolichopodid long-legged flies, 1.7, 0.30), *Lycoriella* (*Lycoriella*) sp. (sciarid, 1.5, 1.0), *Dictyna secuta* Chamberlin (dictynid spider, 3.1, 0.1), *Procaeculus* sp. (caeculid, 3.9, 0.0). The trend of higher abundances in native habitat across all species was highly significant ($p < 0.00001$, one-tailed sign test), although variances were high and few individual comparisons were significant. *Tanytarsus* sp. was the dominant taxon in both habitats, followed by *Dasyhelea* sp. cf. *ancora*, and *Empoasca cerea*, in native vegetation, and *Lycoriella* (*Lycoriella*) sp. and *Limnophyes* sp. in palms. The only introduced species in the samples were the honeybee *Apis mellifera* L. (one in native vegetation) and the German cockroach *Blattella germanica* (L.) (four in native vegetation, one in palms). No species of concern were collected.

Population differences as a function of season and site were minor in comparison to the differences between palm and native habitats. There were a few significant seasonal differences across divergent groups: the family Sciaridae and mites were more abundant in the spring, aphids were completely absent in the spring, and lygaeid seed bugs were more abundant in the fall (Table 2), but sign tests for overall seasonal differences were not significant across taxa in Table 2 ($p = 0.64$). Similarly, the sciarid *Lycoriella* (*Lycoriella*) was more abundant in spring ($p = 0.0075$), but the leafhopper *Empoasca cerea* and the long-legged fly *Sympycnus* sp. cf. *breviventris* occurred only in the fall. There was only one significant Habitat x Season interaction (Lygaeidae), and there were four significant Block effects: for Diptera, the dipteran families Chironomidae and Sciaridae, and the midge *Tanytarsus*.

Linear regression of arthropod assemblage metrics on percent palm green leaves indicated that living and dead palm leaves provided similarly poor habitat for fauna. There were more negative than positive coefficients, but slopes were small, and no models were significant. Results for total individuals (coefficient= -0.0022, p= 0.31, adjusted R^2= 0.019) were representative. Species richness had the strongest response, albeit still non-significant (coefficient= -0.0035, p= 0.083, adjusted R^2= 0.25).

Adults of taxa with aquatic larvae present in springs (Myers and Resh, 2002; Sada et al., 2005) made up a relatively large proportion of our terrestrial collections at 31.0% of total individuals. Taxa with aquatic larvae included the most abundant family in our study, Chironomidae, as well as ceratopogonid biting midges (Table 2), six other dipteran families, and limnephilid northern caddisflies (see Supplementary material).

4. DISCUSSION

Palms appear to have important indirect effects on fauna via replacement of native plants and support of a depauperate arthropod assemblage in comparison to native habitat. There was clearly lower richness, evenness, diversity, and overall abundance as well as lower abundances for individual arthropod families and species in the palms relative to native habitat. Some studies have reported differing responses to woody invasives by different arthropod taxa (e.g., Samways et al., 1996), and we collected some less abundant taxa exclusively in palms, but we would anticipate finding most of these taxa in native vegetation with additional sampling. The influence of introduced palms on the arthropod assemblage appears to be greater than that of native shrub diversity. This effective loss of habitat for fauna as a function of invasion may be important at the landscape scale, because the xeric vegetated habitats that constitute the matrix surrounding isolated springs can have much lower richness and abundance of arthropods than isolated spring riparian areas (Perla and Stevens, 2008). Habitat effects in our study eclipsed the minimal site and season differences. Inter-site differences were minor despite variability in both the native plant assemblage and associated structural complexity. Seasonal effects on fauna were also minimal despite seasonal differences in temperature (~4^{o}C at our sites), moisture (about six times more precipitation in January-March than September-November), and 165 more minutes of photoperiod during March than November. There were essentially no Habitat x Season interactions, indicating that the relative habitat provision of palms and native habitat was consistent and did not shift as a function of seasonal influences.

The depauperate faunal assemblage in the palms was likely due to multiple factors, several of which may be related to replacement of short, structurally complex vegetation with simpler, tall vegetation and a dense canopy. Arthropod diversity and abundance are often correlated with structural complexity of vegetation (Murdoch et al., 1972, Strong et al., 1984, Dennis et al., 1998, Cardoso et al. 2007), both of which are reduced by palms at springs. Shading by invasive trees can also result in impoverished arthropod assemblages (Kinvig and Samways, 2000; Bieringer and Zulka, 2003; Samways and Sharrat, 2010; Samways et al., 2010), and shading in our study was over four times greater under palms than in native habitat, due to both large green leaves and dense skirts of dead leaves (images in Vogl and McHargue, 1966; Cornett, 1987, 2010). Shading can eliminate shorter native vegetation used for perching and oviposition, cause behavioral avoidance of shaded habitats, and/or disrupt development via temperature shifts (Bieringer and Zulka, 2003; Samways and Taylor, 2004;

Smith et al., 2007; Remsburg et al., 2008). Invasive trees can also disrupt movements of flying insects (Wood and Samways, 1991; Smith et al., 2007).

Palm invasion may exert a particularly strong influence on primary consumers. Invasives may support fewer herbivores, because these plants are often selected for their pest-free nature, and/or because invasive plants have expanded their ranges in the absence of herbivores that have had insufficient time to co-evolve in a novel environment (Strong et al., 1984; Tallamy, 2004; Tallamy and Shropshire, 2009). Cornett (2008) reports that isolated, and presumably recently established, fan palm stands lack *Dinapate wrightii* Horn, a palm-boring bostrichid beetle. We found very few herbivores on palms, relative to native plants, possibly because the waxy, robust, and fibrous leaves (Lopez-Llorca and Orts, 1994; Lopez-Llorca et al., 1999) are physically resistant to herbivory or have low nutritional value, or because palm leaves can support mutualistic and entomopathic fungal associates (Lopez-Llorca et al., 1999) and foster antibiotic responses (Dembilio et al., 2009). Reductions in herbivore numbers may in turn cascade into higher trophic levels and the rest of the assemblage, including both invertebrates and vertebrates; ongoing studies of coconut palm invasion in a tropical ecosystem (Senior, 2010) are revealing complex indirect effects involving both fauna and flora.

Observed palm-native differences in arthropod assemblages could have been driven by artifacts, although we think that such error is unlikely to account for much of the observed trend, particularly given the magnitude of differences. It is possible that our necessary catch-per-unit-effort approach was less efficient in palm habitat, but it was no more difficult to systematically work the vacuum nozzle among palm leaves than through native habitat. Coarse structural differences can drive apparent invasive-native differences via habitat selection by arthropods, and a more depauperate odonate assemblage, relative to lower plant structure, has been found among both invasive and native trees (Smith et al., 2007). Our one site that was dominated by native trees, however, had arthropod assemblage metrics that varied from average (for native habitat) to near the high end of the range. Further, the palm-native differences were consistent with both our visual observations of arthropods and with collections from beating samples taken during our pilot explorations of the two habitats.

The proportion of adults from taxa with aquatic larvae were about an order of magnitude higher in our desert springs than in some "wetter" wetlands, and this phenomenon may be indicative of the relative isolation of the springs. Adult phases of aquatic insects comprised 31% of our terrestrial spring fauna, but Holmquist et al. (2010) found only 2.7% of the terrestrial fauna from wet meadows in the Sierra Nevada mountains to be comprised of adults derived from aquatic larvae, and other work in both wet meadows and fens has yielded similar results (1.3% and 3.9%, respectively, Holmquist et al., submitted). Wet meadows and fens produce large numbers of aquatic insects that have terrestrial adult phases (Batzer and Wissinger, 1996; Wissinger et al., 1999; Holmquist et al., submitted), and yet there is apparently high export of adults to other habitats. The high relative abundance of terrestrial adult phases of aquatic taxa in our desert spring samples could be a function of low abundance of taxa that are wholly terrestrial but also suggests high fidelity of aquatic taxa to isolated spring habitat. Mitochondrial DNA sequencing provides strong evidence for varying degrees of isolation for selected caddisflies inhabiting desert springs (Myers et al., 2001). Export of adults to other habitats may be low due to the xeric matrix (Shepard, 1993; Tiner, 2003; Perla and Stevens, 2008) that surrounds the desert springs, resulting in high contrast boundaries with low permeability (Wiens et al., 1985; Stamps et al., 1987; Holmquist, 1998) and ultimately low connectivity with other springs and other habitats (Myers and Resh, 1999; Tiner, 2003; see also Crooks and Sanjayan, 2006).

The small size and isolation of spring riparian habitats exacerbates vulnerability to disturbance (Shepard, 1993; Myers et al., 2001; Fleishman et al., 2006, Hendrickson et al., 2008). Negative effects of water withdrawal and other stressors (Myers and Resh, 1999; León de la Luz and Domínguez, 2006; Unmack and Minckley, 2008) may be worsened by invasive palms. Palms are significant competitors for water, light, and soil space (Vogl and McHargue, 1966; Cornett, 1985, 2008; Kelly, 2007; Unmack and Minckley, 2008), and our results are consistent with the observation that palms are most likely to invade wetter sites that support high plant diversity. Further, habitat quality for fauna appears to be severely reduced via monopolization by palms, effectively further reducing the size of already small habitat patches for fauna.

Palm control efforts at springs (Kelly, 2007; Kodric-Brown et al., 2007) usually result in dead "ghost palms" that are left in place (Kelly, 2007) and can remain standing for thirty years (J.W. Cornett, pers. comm.). Ghost palms are likely to continue to negatively affect arthropods, because the attached dead leaves should have similar (low) habitat quality as the dead leaves that are attached to living palms, and because leaf skirts and fallen thatch will persist for many years in arid environments and continue to preclude recruitment of native vegetation (Vogl and McHargue, 1966). Rehabilitation of both native flora and fauna should be part of the restoration process (Samways and Sharratt, 2010). Increases in some indigenous arthropod taxa can be achieved more effectively by removal of alien tree canopies and increasing light penetration than by provision of understory vegetation (Remsburg et al., 2008), and some indigenous arthropods are found only where invasive trees have been removed (Samways et al., 2005; but see Samways, 2003). Although the necessity and practicality of palm control can be debated (Cornett, 2010), if control efforts are to be undertaken, we suggest complete removal of ghost palms to allow recovery of the desert spring assemblage. Further, any removal of palms should be incremental, so that habitat is not drastically and suddenly altered (Samways and Sharratt, 2010). We also suggest tracking response of native vegetation and fauna to these efforts, because recruitment to isolated springs may be relatively slow for fauna without winged adult forms and for winged forms with poor capability for dispersal across harsh desert expanses (Myers et al., 2001).

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Table 1 Means, standard errors, and p-values from 1x2 blocked ANOVAs with repeated measures for assemblage-level faunal metrics. All metrics are based on one-minute vacuum samples.

		Native		Palm		ANOVA			
		Mean	SE	Mean	SE	Habitat	Season	Habitat x Season	Block
Total individuals	Spr	45.3	15.8	7.10	1.91	0.00022**	0.90	0.26	0.029*
	Fall	38.5	17.1	7.50	1.49				
Species richness	Spr	14.7	2.96	4.70	1.27	0.00031**	0.62	0.26	0.075
	Fall	10.2	2.38	4.30	0.70				
Expected no. of species	Spr	1.90	0.031	1.41	0.252	0.053	0.30	0.23	0.46
	Fall	1.85	0.034	1.71	0.102				
Family richness	Spr	12.2	2.15	4.40	1.19	0.00047**	0.66	0.21	0.091
	Fall	8.30	1.54	4.20	0.66				
Probability of inter-specific encounter	Spr	0.841	0.030	0.541	0.121	0.0057**	0.92	0.45	0.25
	Fall	0.766	0.031	0.598	0.087				
% Dominance	Spr	25.6	4.29	40.8	9.74	0.12	0.27	0.70	0.58
	Fall	33.4	4.39	48.3	8.98				
% Herbivores	Spr	32.6	7.84	14.5	3.78	0.029*	0.79	0.055	0.37
	Fall	47.4	9.01	15.6	5.07				

% Predators	Spr	24.3	5.91	36.9	11.8	0.30	0.075	0.36	0.37
	Fall	31.1	8.17	46.7	10.6				
% Other feeding groups	Spr	43.1	6.68	48.6	10.5	0.43	0.11	0.68	0.23
	Fall	21.5	6.99	37.7	9.15				

* and ** flag p-values less than 0.05 and 0.01, respectively.

Table 2 Mean abundances, standard errors, and p-values from 1x2 blocked ANOVAs with repeated measures for orders and ten most abundant families. All metrics are based on one-minute vacuum samples.

		Native		Palm		ANOVA			
		Mean	SE	Mean	SE	Habitat	Season	Habitat x Season	Block
Thysanura	Spr	0.00	0.00	0.00	0.00	NA			
	Fall	0.00	0.00	0.10	0.10				
Orthoptera	Spr	0.10	0.10	0.20	0.20	0.85	0.79	0.49	0.67
	Fall	0.40	0.40	0.10	0.10				
Blattodea	Spr	0.00	0.00	0.10	0.10	0.63	0.60	0.20	0.59
	Fall	0.40	0.40	0.00	0.00				
Hemiptera	Spr	12.1	4.40	0.90	0.35	0.0011**	0.52	0.73	0.72
	Fall	13.5	4.34	1.10	0.41				
Miridae	Spr	2.60	1.57	0.00	0.00	0.022**	0.49	0.49	0.50
	Fall	3.70	1.78	0.00	0.00				
Lygaeidae	Spr	0.20	0.13	0.00	0.00	0.032**	0.019*	0.019*	0.50
	Fall	1.90	0.80	0.20	0.20				
Cicadellidae	Spr	1.90	0.97	0.10	0.10	0.0035**	0.20	0.20	0.77
	Fall	5.70	2.42	0.10	0.10				

Aphididae	Spr	4.20	2.89	0.40	0.22	NA			
	Fall	0.00	0.00	0.00	0.00				
Thysanoptera	Spr	0.60	0.50	0.00	0.00	NA			
	Fall	0.00	0.00	0.00	0.00				
Coleoptera	Spr	1.00	0.37	0.40	0.27	0.46	0.54	0.29	0.49
	Fall	0.50	0.34	0.60	0.40				
Neuroptera	Spr	0.50	0.22	0.10	0.10	0.048**	0.13	0.49	0.37
	Fall	0.20	0.13	0.00	0.00				
Hymenoptera	Spr	4.00	1.32	0.20	0.20	0.0071**	0.20	0.12	0.53
	Fall	0.80	0.25	0.30	0.21				
Trichoptera	Spr	0.00	0.00	0.00	0.00	NA			
	Fall	0.00	0.00	0.10	0.10				
Lepidoptera	Spr	0.80	0.25	0.10	0.10	0.0029**	0.12	0.32	0.51
	Fall	0.30	0.15	0.00	0.00				
Diptera	Spr	19.7	8.81	3.60	1.19	0.0064**	0.18	0.20	0.0083**
	Fall	15.8	12.0	3.70	1.62				
Ceratopogonidae	Spr	5.20	3.23	0.30	0.21	0.24	0.071	0.13	0.46
	Fall	0.40	0.40	0.20	0.20				
Chironomidae	Spr	6.80	3.80	0.60	0.40	0.035*	0.65	0.36	0.013*
	Fall	11.2	9.99	2.10	1.38				

Sciaridae	Spr	2.50	1.18	1.30	0.40	0.78	0.0046**	0.85	0.035*
	Fall	0.10	0.10	0.10	0.10				
Tethinidae	Spr	1.50	0.72	0.10	0.10	0.046*	0.92	0.19	0.41
	Fall	1.00	0.52	0.50	0.31				
Araneae	Spr	1.90	0.89	1.30	0.50	0.42	0.12	0.36	0.81
	Fall	4.80	3.15	1.50	0.45				
Dictynidae	Spr	0.10	0.10	0.00	0.00	0.15	0.13	0.23	0.59
	Fall	3.00	2.56	0.10	0.10				
Acari	Spr	4.80	1.97	0.10	0.10	0.031*	0.025**	0.054	0.45
	Fall	2.50	2.19	0.00	0.00				
Caeculidae	Spr	1.70	1.29	0.00	0.00	0.20	0.36	0.36	0.50
	Fall	2.20	2.20	0.00	0.00				
Pseudoscorpiones	Spr	0.00	0.00	0.00	0.00	NA			
	Fall	0.10	0.10	0.00	0.00				

NA insufficient data to test

* and ** flag p-values less than 0.05 before and after, respectively, sequential Bonferroni correction for all taxa within a given order.

FIGURE CAPTION

Fig. 1 Rank abundance plot for families, comparing palm and native habitat. Based on total abundances for study.

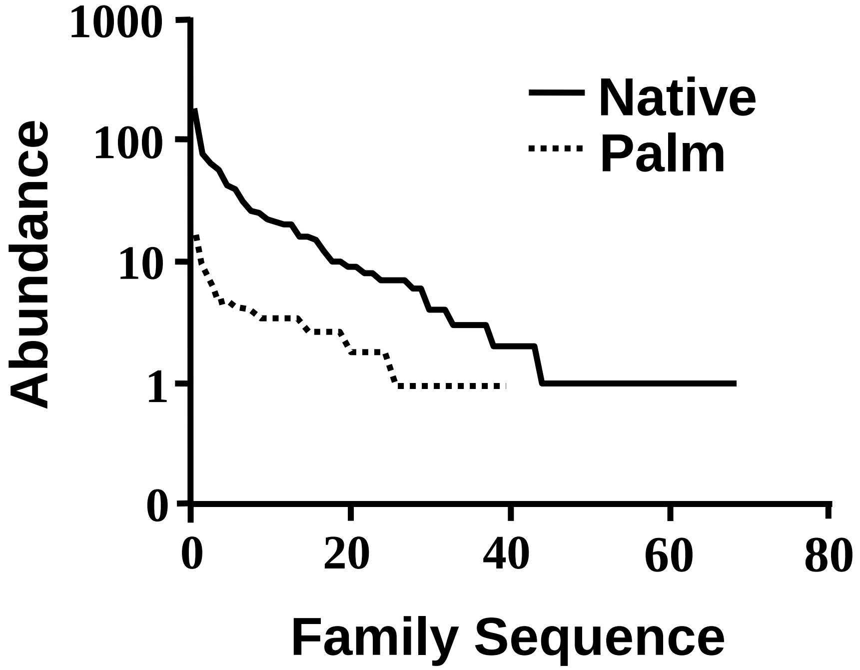
1000
100
10
1
0
Abundance
Native
Palm
0
20
40
60
80
Family Sequence

Figure 1

SUPPLEMENTARY MATERIAL

Appendix Overview of fauna and distribution by habitat. Inequalities do not indicate statistical differences.

Thysanura		Neuroptera		Diptera cont'd.	
Lepismatidae	p	Coniopterygidae	n=p	Bombyliidae	N
Orthoptera		Chrysopidae	n	Empididae*	P>n
Acrididae	n	Hymenoptera		Dolichopodidae*	N>>p
Gryllidae	P	Ceraphronidae	p	Phoridae	n
Blattodea		Evaniidae	n	Muscidae*	n
Blattellidae	N>p	Braconidae	n	Tephritidae	N
Hemiptera		Ichneumonidae	n	Chamaemyiidae	p
Reduviidae	n	Mymaridae	N	Agromyzidae	n
Miridae	N	Encyrtidae	n	Chloropidae	N>>P
Nabidae	N>p	Pteromalidae	N>>P	Tethinidae	N>P
Pentatomidae	N	Platygastridae	N	Heleomyzidae	P>n
Berytidae	n	Halictidae	n	Drosophilidae	N>P
Rhyparochromidae	P	Apidae	n	Araneae	
Lygaeidae	N>>P	Formicidae	N>>p	Pholcidae	P
Rhopalidae	P	Trichoptera		Araneidae	N>P
Cicadellidae	N>>P	Limnephilidae*	p	Linyphiidae	p
Cixiidae	N>>P	Lepidoptera		Dictynidae	N>>p
Issidae	N	Gracillaridae	N	Lycosidae	p
Psyllidae	N	Coleophoridae	N	Anyphaenidae	P>>n
Aphididae	N>>P	Gelechiidae	N	Philodromidae	N
Thysanoptera		Pyralidae	n	Thomisidae	N>>P
Thripidae	N	Lycaenidae	n	Salticidae	N>P
Coleoptera		Geometridae	n=p	Acari	
Staphylinidae	n	Diptera		Erythraeidae	N
Limnichidae	P	Tipulidae*	N=P	Caeculidae	N
Cleridae	N	Ceratopogonidae*	N>>P	Unknown Acari	N>>P
Melyridae	N	Chironomidae*	N>>P	Pseudoscorpiones	
Coccinellidae	P	Simuliidae*	n	Cheliferidae	n
Mordellidae	N	Cecidomyiidae	n		
Bruchidae	P>N	Scatopsidae	N		
Chrysomelidae	N	Sciaridae	N>P		
Curculionidae	N	Stratiomyidae*	n		

N and P two or more individuals found in native or palm habitat, respectively; presence of a single letter indicates that the family was found in only the indicated habitat.

n and p a singleton in either native or palm habitat, respectively.

\> habitat to left of sign had more abundance than the habitat to the right of the sign.

\>> habitat to left of sign had more than five times the abundance than the habitat to the right of the sign.

= equal number of individuals in the two habitats.

* aquatic as larvae