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 10 springs in Death Valley National Park, California, USA, during both spring and fall growing seasons using suction sampling. The invading palms *Phoenix dactylifera* L. and *Washingtonia filifera* (Linden ex André) 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.

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 Sharratt (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

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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 Mojave 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 °C, with a record of 57 °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 10 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; Törmälä, 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 0.25 mm 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