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THE ROLE OF HOST IDENTITY IN DETERMINING THE DISTRIBUTION OF THE INVASIVE MOTH *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) IN FLORIDA

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Abstract

We examined the association between the exotic South American cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), and its host plants (prickly pear cacti, subfamily Opuntioideae) in Florida to assess the role of host plant identity and local host community on the prevalence of this invasive moth. From May to September 2008, we surveyed 4,243 plants across 165 sites throughout Florida for *C. cactorum*. The probability of *C. cactorum* presence at a particular site was best explained by the presence of either *Opuntia humifusa* var. *ammophila* (Small) L. D. Benson or *O. stricta* (Haworth) Haworth. Within infested sites, only *O. stricta* individuals were significantly more infested than other host plants. Our results suggest that understanding patterns of *C. cactorum* infestation, both in Florida and as it spreads towards the western United States relies, at least in part, on determining the mechanism by which *O. stricta* influences the suitability of specific host communities.

Key Words: diversity, Florida, invasive species *Opuntia* plant-insect interactions

Resumen

Se examinó la asociación entre la polilla exótica del nopal de América del Sur, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), y sus plantas hospederas (nopal, subfamilia Opuntioideae) en la Florida para evaluar el efecto en la identidad (especie) de la planta hospedera y la comunidad de la flora local sobre la prevalencia de esta polilla invasora. Desde mayo hasta septiembre 2008, revisamos 4,243 plantas en 165 sitios en toda la Florida para *C. cactorum*. La probabilidad de la presencia de *C. cactorum* en un sitio particular se explica mejor por la presencia de *Opuntia humifusa* var. 'ammophila' (Small) L.D. Benson u *O. stricta* (Haworth) Haworth. Dentro de los sitios infestados, solamente las plantas de *O. stricta* fueron significativamente más infestadas que las otras plantas hospederas. Nuestros resultados sugieren que al entender los patrones de infestación de *C. cactorum*, tanto en la Florida asi como el incremento en su rango hacia el oeste de Estados Unidos se basa, por lo menos en parte, en la determinación del mecanismo por el cual *O. stricta* influye en la migración de *Cactoblastis cactorum* a las comunidades específicas de plantas hospederas.

Palabras clave: diversidad, La Florida, especies invasoras; *Opuntia*, interaccion planta-insecto

The quality and availability of resources are key factors that define opportunities for consumers to invade and persist in certain communities (Andow 1991; Ostfeld & Keesing 2000a, 2000b). Numerous studies have shown that various resource characteristics can influence the establishment and abundance of potential invaders such as microbial pathogens (Holt et al. 2003), plants (Davis et al. 2000), and animals (Andow 1991; Barbosa et al. 2009). The consequence of local host community heterogeneity for exotic consumers is that certain host species may be of sufficiently low quality that they cannot sustain consumer populations in the absence of higher quality host species. Even where hosts are capable of sustaining consumer populations, variation in host quality can lead to associational resistance or associational susceptibility. If the consumer cannot accurately perceive host quality, a high density of relatively low quality hosts in the community may

lead to resistance by association: lower consumer population sizes and a consequent reduction in the consumer's impact on higher quality species in the community (Andow 1991; Holt et al. 2003). In contrast, high densities of relatively high quality hosts can induce associational susceptibility for lower quality hosts in the local community (Andow 1991). Consequently, the identities of the host species present in a community and the relative quality of those hosts to the consumer are important in determining whether consumer impact will be high or low in local host communities (LoGiudice et al. 2003; Power & Mitchell 2004; Russell et al. 2007; Brooks & Zhang 2010).

Our goal was to assess the role of host species and community structure on the distribution of the exotic South American Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), across the state of Florida. *Cactoblastis cactorum* is a multivoltine pyralid moth that specializes on prickly pear cacti (subfamily Opuntioideae) and has been widely used as a biological control agent for invasive prickly pear cacti in countries such as Australia (Dodd 1940) and South Africa (Pettey 1948). After it was introduced to the island of Nevis for biological control of native *Opuntia* (Simmonds & Bennett 1966), *C. cactorum* subsequently spread throughout the Caribbean and was first detected in North America in the Florida Keys in 1989 (Dickel 1991). In the United States, this invasion has since spread as far north as Charleston, South Carolina along the Atlantic Coast (Hight et al. 2002) and as far west as Cameron Parish, Louisiana along the Gulf of Mexico (Rose 2009a). The moth feeds on a wide array of taxa within the Opuntioideae subfamily, including all 6 known native and 3 introduced taxa found in Florida (Johnson & Stiling 1998; Hight et al. 2002; K. Sauby & T. Marsico, personal observations). At least 46 species in the Opuntioideae subfamily have been found to be hosts for *C. cactorum* based on observations of herbivory in the field (reviewed by Sauby 2009). Based on laboratory studies, *C. cactorum* is also capable of producing viable adults from 2 additional cactus species, *Cylindropuntia acanthocarpa* (Engelmann and Bigelow) F. M. Knuth and *C. spinosior* (Engelmann) F. M. Knuth (Jezorek et al. 2010), that have not been reported to be selected as host taxa in the field.

We were interested in addressing the role of various host species and the structure of local host communities on cactus moth prevalence by determining factors associated with the probability of infestation at sites across the state of Florida. Subsequently, we wished to describe any traits that might explain individual-level patterns of infestation within sites containing *C. cactorum*. The native *Opuntia stricta* (Haworth) Haworth has previously been implicated as a preferred host species in Florida (Baker & Stiling 2008) and in the Caribbean (Pemberton & Liu

2007). *Opuntia stricta* was also the main species targeted and brought under control by *C. cactorum* in Australia (Dodd 1940). Additionally, the *C. cactorum* population that ultimately invaded Florida was introduced to the Caribbean from a population in South Africa that itself originated from the Australian biological control efforts (Pettey 1948; Simmonds & Bennett 1966; Marsico et al. 2011). Therefore, we hypothesized that the presence of *O. stricta* at a site would increase the likelihood of infestation and that, within infested sites, we would observe the highest prevalence of *C. cactorum* on *O. stricta*.

Species can influence the probability of infestation at a particular site as a result of either serving as a strong attractant to dispersing females or because their high nutritional quality leads to greater fitness on some host species than others (i.e., a reservoir). Predictions about preferences among ovipositing females based on laboratory and field-based data are inconsistent, especially for taxa found in Florida (Robertson 1987; Johnson & Stiling 1996; Mafokoane et al. 2007; Tate et al. 2009; Jezorek et al. 2010), even though host species are found to significantly differ in quality as measured by survivorship and fecundity (Pettey 1948; Robertson 1987; Johnson & Stiling 1996; Mafokoane et al. 2007, but see Woodard et al. 2012). We predict that most host species would be relatively poor hosts for the exotic moth and that the prevalence of *C. cactorum* would be lower at sites with greater species diversity.

Infestation of individuals within sites is expected to depend on physical attributes of the hosts. For example, the amount of plant biomass available (as reflected by the size of plants) to support herbivore populations may lead to greater infestation over time. Additionally, evidence suggests that adult females choose host plants through the use of CO_2 (Stange et al. 1995) and volatile organic compound (VOC) gradients near host plants that are of a certain height (Pophof et al. 2005). Thus, plant height may be an important factor determining the likelihood that a plant will be infested by *C. cactorum*. Consequently, we predicted that larger host species would be better hosts for the exotic moth and that *C. cactorum* infestations would be more likely at sites with larger *Opuntia* host species.

MATERIALS AND METHODS

Study Sites and Data Collection

From May to September 2008, 4,243 plants across 165 sites throughout Florida were surveyed for the presence of *C. cactorum* (Figs. 1 and 2). Sampling was restricted to the region of Florida east of Pensacola Beach because all points west were actively managed by the United States De-

partment of Agriculture (USDA) for *C. cactorum* through removal of *Opuntia* spp. from public and private land (Rose 2009b). Because of the patchy nature of *Opuntia* in the state and our goal of coverage at such a large spatial scale, sites were not chosen at random. Instead, we performed roadside surveys and, after consultation with rangers and biologists, surveyed sites on public lands (state parks, state forests, national forests, and a national wildlife refuge) where cacti were known to occur. At each site, we visually identified the extent of the patch and established a transect through the patch. All host plants along the transect were identified to species (or variety, if applicable) and inspected for the presence of *C. cactorum* larvae. Taxonomic delineations for cacti were based on those by Pinkava (2003), except for the 3 varieties of *O. humifusa* (Rafinesque) Rafinesque, for which we relied on Benson (1982) and expert opinion (Lucas C. Majure, Dept. of Biology, University of Florida, personal communication). Height was measured for every fifth plant of each taxon detected along the transect. Because host plant density varied among sites and taxa, sampling for *C. cactorum* was limited at each site to a maximum of approximately 2 h.

All plants' cladodes along each transect were examined for evidence of *C. cactorum* infestation, including entry holes, eggsticks, frass (green to brown excrement exuding from entry holes), and/ or hollowed or translucent cladodes. Because larvae of the native cactus moth, *Melitara prodenialis* Walker, also feed internally and produce similar signs of damage, all cladodes showing evidence of infestation were dissected to confirm the presence and identity of moth larvae. A late-instar larva of *C. cactorum* has an orange body and dorsolateral black bands or transverse spots on the abdomen. In contrast, a late-instar *M. prodenialis* larva has a dark blue to brown body (Neunzig 1997). However, early-instar larvae are difficult to distinguish by morphology alone. Therefore, larvae which could not be confidently identified by morphology alone were identified using molecular methods as described in Marsico et al. (2011).

Statistical Analysis

All analyses were conducted using the R Statistical Language (R Development Core Team, 2009). Maps were generated using ArcGIS Version 10 (ESRI, 380 New York Street, Redlands, CA 92373).

Factors Affecting the Probability of *Cactoblastis cactorum* Presence at Sites

We assessed the effects of individual host taxa and the local host community on the probability of a site being infested with *C. cactorum*. First, we used the binomial distribution to calculate the minimum number of plants that we would need to sample in order to minimize the probability of erroneously designating a site as uninfested (when in fact *C. cactorum* was present) to less than or equal to 0.05. The probability of success used in this calculation was the proportion of plants infested by *C. cactorum* at sites where the moth was known to be present. Based on this analysis, we determined that a minimum of 30 plants would need to be sampled to have confidence that we did not erroneously designate a site as uninfested. Thus, we only included sites in which we were confident that the moth was present (*C. cactorum* was detected; $n = 39$) or absent (where at least 30 plants were inspected with none being infested; $n = 34$) in our assessment of factors correlated with the presence/absence of *C. cactorum* at a site.

We also examined the influence of host taxon evenness and richness on *C. cactorum* site prevalence (the proportion of plants infested by *C. cactorum* at a site). Host taxon evenness was calculated using Simpson's Index (Simpson 1949; Smith & Wilson 1996). Evenness was calculated only for sites that had sufficiently large number of plants inspected and where more than one host taxon was found ($n = 22$). A generalized linear mixed model (binomial family with a logit link and site identity included as a random effect) was used to examine whether *C. cactorum* presence at a site could be predicted by the host taxon richness or evenness at that site, or by the presence of the 4 most abundant host species (*O. humifusa* var. *ammophila* (Small) L. D. Benson, *O. humifusa* var. *humifusa*, *O. pusilla* (Haworth) Haworth, and *O. stricta*). Because richness had a maximum of only 3 species at any site, we also used a binomial test to determine whether polyculture sites (defined as the sites in which at least 2 species had a relative frequency greater than 5%, $n = 21$) had a different probability of being infested than monoculture sites (defined as the sites in which only one species had a relative frequency greater than 5%, $n = 52$). Additionally, for each of the 4 most abundant host taxa, we performed a binomial test (with a Bonferroni correction for the probability of a Type I error to account for the multiple tests) to determine whether *C. cactorum* was found more often than by chance in sites with a particular host taxon compared to sites without. Finally, we performed separate Mann-Whitney U tests to determine if *O. stricta* and *C. cactorum* were detected more closely to the coast of Florida than predicted by chance.

Factors Affecting the Patterns of Infestation Where *Cactoblastis cactorum* is Present

For sites where *C. cactorum* was known to be present, host plant identity and height were evaluated as predictors of infestation for indi-

vidual plants using a generalized linear mixed model (binomial family with a logit link and site identity included as a random effect). A binomial test was used to assess whether the probability of infestation for plants of different species differed from the state-wide proportion of infested plants across all infested sites (p = 0.0952). To ensure that sample sizes were large enough for comparisons, this analysis was restricted to host taxa that were found at 15 or more sites and had height measurements for a minimum of 50 individuals: *O. humifusa* var. *ammophila*, *O. humifusa* var. *humifusa*, *O. pusilla*, and *O. stricta*. A comparison of median plant heights was conducted by log transforming the data to normality and then conducting a Welch's two-sample t-test to assess whether there was a significant difference between the height of plants with (*n* = 72) and without *C. cactorum* (n = 556).

<center>RESULTS</center>

Nine potential host taxa (excluding one unidentified Opuntioid plant in Key Largo) were identified at sites surveyed throughout Florida (Table 1). Of these, 6 were infested with *C. cactorum*: the introduced taxa *Nopalea cochenillifera* (L.) Salm-Dyck and *O. ficus-indica* (L.) Miller and the native taxa *O. humifusa* var. *ammophila*, *O. humifusa* var. *humifusa*, *O. pusilla*, and *O. stricta*. No infested plants were found from 3 taxa: *Opuntia humifusa* var. *austrina,* O. *triacantha* (Willdenow) Sweet, and *O. engelmannii* Salm-Dyck ex. Engelmann. However, all of the identified taxa have previously been found to be infested by *C. cactorum* (Johnson & Stiling 1998; Baker & Stiling 2008; T. D. Marsico, personal observations).

Factors Affecting the Probability of *Cactoblastis cactorum* Presence at Sites

Cactoblastis cactorum was found at 53% of sites with a sufficiently large sample size to accurately determine absence (24% of all sites surveyed, Fig. 1). At infested sites, the *C. cactorum* site prevalence ranged from 1.1% to 71.4%, with an average of 9.52% plants infested. The *C. cactorum* site prevalence was higher at sites that included either the host taxa *O. stricta* (p = 0.001) or *O. humifusa* var. *ammophila* (p = 0.014, Fig. 2). Infested sites were significantly closer to the coast of Florida (median distance from coast of 0.4 km for infested sites versus 28.7 km for uninfested sites; p < 0.001; U-test), but *O. stricta* was also restricted to near-coast locations (median of 0.28 km from the coast for sites containing *O. stricta* compared to 47.45 km for those without the species present; p < 0.001; U-test). In contrast, *O. humifusa* var. *ammophila* has a more inland distribution (median of 28.39 km from the coast for sites containing *O. humifusa* var. *ammophila* compared to 0.499 km for those without the species present; Fig. 2). There were only 3 sites where *C. cactorum* was found and neither *O. humifusa* var. *ammophila* nor *O. stricta* were found; these 3 sites contained monocultures of *O. humifusa* var. *humifusa*.

We did not find a relationship between richness or Simpson's Index and *C. cactorum* site prevalence at polyculture sites (p = 0.93). Additionally, the probability that a site would be infested by *C. cactorum* was not higher for polyculture sites compared with monocultures (p = 0.055, binomial test).

Factors Affecting the Patterns of Infestation Where *Cactoblastis cactorum* is Present

Neither host plant identity nor height were significant predictors of *C. cactorum* infestation within a site. However, within infested sites, the height of plants found infested with *C. cactorum* was significantly greater than the height of plants on which *C. cactorum* was not detected (median infested plant height = 41 cm, median uninfested plant height = 20 cm; p < 0.001, U-test, Fig. 3). Likewise, individuals of 2 species, *O. stricta* and *O. humifusa* var. *ammophila*, were more likely to be infested than expected when they were found in sites that contained *C. cactorum* (p < 0.01 for both, binomial test).

TABLE 1. THE NINE SPECIES OF *OPUNTIA* THAT WERE IDENTIFIED ACROSS THE STATE OF FLORIDA AND THE PATTERNS OF USE BY *CACTOBLASTIS CACTORUM*.

Genus	Species	Variety	Pr[infested]	*n*
Nopalea	*cochenillifera*		0.029	34
Opuntia	*engelmannii*		0.000	74
	ficus-indica		0.054	37
	humifusa	*ammophila*	0.049	467
	humifusa	*austrina*	0.000	299
	humifusa	*humifusa*	0.010	1562
	pusilla		0.004	520
	stricta		0.071	1240
	triacantha		0.000	9

The sample size (*n*) shows the number of plants inspected across the state and Pr [infested] shows the proportion of plants across the state that were infested.
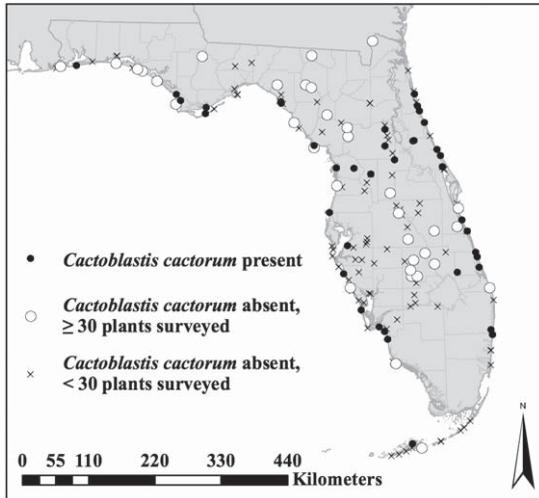
Fig. 1. Sites surveyed in Florida where *Cactoblastis cactorum* was present (*n* = 39), absent and 30 more more plants were surveyed (*n* = 34), and absent and less than 30 plants were surveyed (*n* = 92).

DISCUSSION

Our results suggest that *C. cactorum* prevalence is highest on 2 taxa, *O. stricta* and *O. humifusa* var. *ammophila*, and in local host communities that include either of these species. The average site prevalence of *C. cactorum* was not significantly greater in host taxa polycultures compared to host monocultures. The failure to find a significant relationship between host taxon evenness and *C. cactorum* site prevalence suggests that highly competent host taxa like *O. stricta* and *O. humifusa* var. *ammophila* may drive the infestation of other taxa even when present at low relative abundances in a community. While we cannot disentangle whether the preference for sites with *O. stricta* was an artifact of the proximity to the coast, or whether the coastal distribution was a consequence of habitat suitability of the host plant, the apparent suitability of a more inland distributed species, *O. humifusa* var. *ammophila*, suggests that the host taxon may be more influential than proximity to coast in determining the risk of infestation. This has implications for predicting the future spread of *C. cactorum*. Our ability to predict the potential spread of *C. cactorum* in North America may reside in our ability to elucidate the important traits associated with influential hosts that can be used to refine our predictions rather than reliance upon environmental models that correlate with the distribution of all *Opuntia* (Brooks et al. 2012).

Recent attention has been focused on the impact of resource diversity on consumer dynamics (e.g., Barbosa et al. 2009; Keesing et al. 2010). In many cases, the presence of a particularly in-
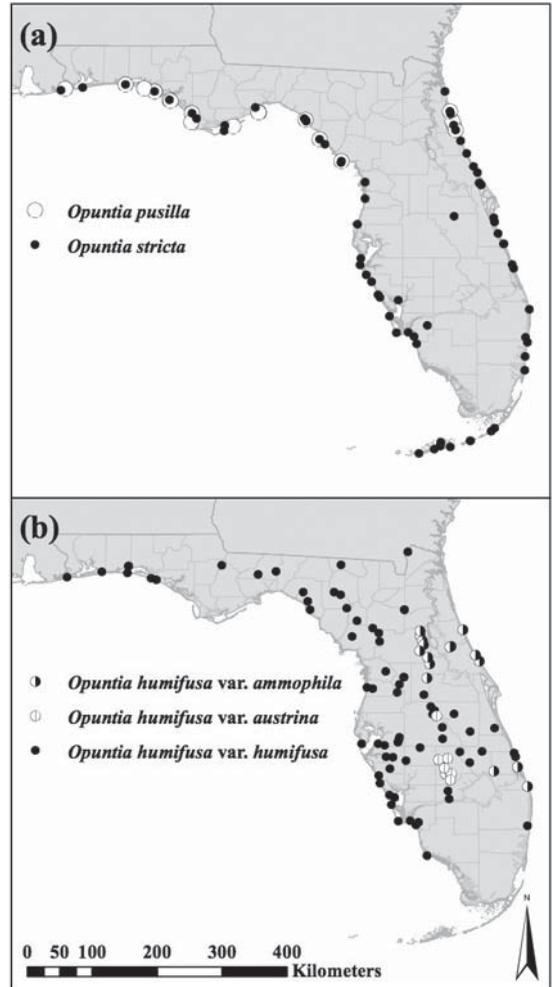

Fig. 2. Common native host plant taxa found in Florida included (a) *Opuntia stricta* (*n* = 68 sites) and *Opuntia pusilla* (*n* = 19 sites) as well as (b) 3 varieties of *Opuntia humifusa*: var. *ammophila* (*n* = 16 sites), var. *austrina* (*n* = 9 sites), and var. *humifusa* (*n* = 70 sites).

fluential species in a community can be more influential than diversity *per se* (e.g., in terms of primary productivity [Tilman et al. 1997; Paine 2002] or resistance to invasion [Emery & Gross 2007]). The tendency for more species-rich communities to include such influential taxa (often referred to as a "sampling effect" because there is an increased probability of sampling common species with increased species richness) can be a confounding factor when attempting to assess the impact of diversity *sensu stricto* (Aarssen 1997; Huston 1997; Tilman et al. 1997). A significant increase in the probability of infestation at sites including *O. stricta* and/or *O. humifusa* var. *ammophila* regardless of species diversity suggests that there is not an effect of diversity in Florida where diversity at any site is low.
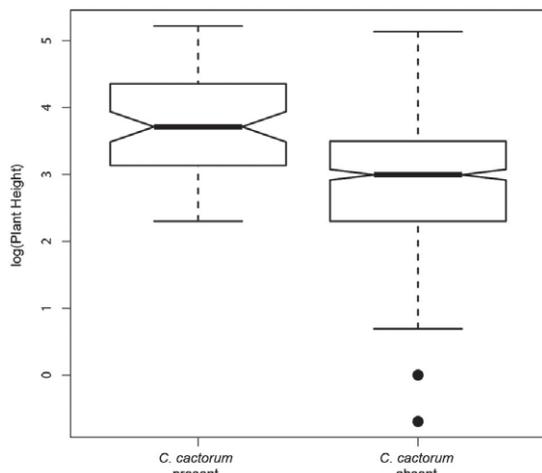
Fig. 3. A boxplot showing the log of host plant height (cm) that were either found to be infested (*n* = 72) or uninfested (*n* = 556) with *Cactoblastis cactorum* across all infested sites.

Patterns of *C. cactorum* prevalence also appear to be influenced by factors such as plant height. Plants on which *C. cactorum* was detected were significantly taller than those on which *C. cactorum* was not found. The presence of taller plant species may signify greater biomass availability or may influence the "apparency" (*sensu* Feeny 1976) of cactus patches for dispersing females. For example, evidence suggests that adult females choose host plants through the use of CO_2 (Stange et al. 1995) and volatile organic compound (VOC) gradients near host plants (Pophof et al. 2005). Thus, the apparency of a particular host plant may be dependent upon its detectability through a combination of both VOCs and CO_2 gradients. Taller plants, up to a certain height, may be more apparent than smaller plants because they fix CO_2 and release VOCs over a larger surface area. Within a given height range, host taxa may differ in terms of apparency to *C. cactorum* if they differ in qualitative aspects of VOC emissions. However, nothing is currently known about variation in CO_2 and VOC emissions among native cacti in Florida.

It is worth noting that the present study describes the patterns of infestation over a large spatial extent, but that the data presented here were collected within a single year. Additional sampling would be needed to determine temporal patterns of infestation, such as how the intensity and locations of *C. cactorum* infestations vary seasonally and yearly, and why *C. cactorum* was found at some inland sites and not others. We also recognize that our sampling strategy is biased against small populations that are difficult to detect and against populations outside of park boundaries. This bias represents the current knowledge of *Opuntia* spp. distributions in Florida. Before this study, information about the statewide distributions of cacti was limited to county presence/absence data and the locations recorded on museum vouchers. Therefore we relied on roadside surveys and ranger/biologist expert opinions to select study sites.

CONCLUSIONS

While the identification of *O. stricta* as a preferred host is unsurprising (e.g., Baker & Stiling (2008) found that *O. stricta* was more frequently infested with *C. cactorum* than *O. humifusa* in Florida), we are unaware of any other studies that have reported on the significant degree of heterogeneity in *C. cactorum* infestation among the 3 varieties of *O. humifusa*. The fact that *O. humifusa* var. *ammophila*, in addition to *O. stricta*, appears to be an influential taxon in terms of *C. cactorum* prevalence, whereas *O. humifusa* var. *humifusa* and *O. humifusa* var. *austrina* do not, underscores the importance of recognizing systematic differences among host taxa and among individuals within a given taxon (e.g., Majure et al. 2012). While *O. humifusa* var. *ammophila* does appear to be an influential taxon in terms of *C. cactorum* infestation in Florida, it is endemic to Florida and therefore is unlikely to be as important in driving the North American range expansion of *C. cactorum* as *O. stricta*. However, the identification of multiple influential hosts is important to our understanding of the future spread of *C. cactorum* because of the potential insights it may provide into host traits that may limit its spread in North America.

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