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Biotic constraints on *Cactoblastis cactorum* (Berg) host use in the southern US and their implications for future spread

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ABSTRACT

The roles of biotic interactions in determining invasion success emerge from the set of traits possessed by the invader and those present in the community being invaded. Identifying traits important for governing invader distributions is challenging, but systems in which invaders specialize on hosts or resources may facilitate narrowed focus on particular suites of traits. Most examples of specialist consumers that become successful invaders are escaped biological control species. One example is the South American cactus moth (*Cactoblastis cactorum*), an escaped biological control agent that infests prickly-pear cacti (primarily taxa in the genus *Opuntia*). Here we quantify tissue macronutrient traits (crude fiber, lipid, crude protein, and carbohydrate by difference) and evaluate *C. cactorum* infestation of several North American *Opuntia* taxa as a function of those traits. We then evaluate whether a common, native cactus moth (*Melitara prodenialis*) infests plants that are similar to those used by *C. cactorum* to evaluate the likelihood that the species compete for hosts. Our results generally suggest that *Opuntia* tissue macronutrients may be important traits in mediating cactus moth-*Opuntia* associations. While the range of macronutrients that are suitable for *M. prodenialis* are largely similar to those for *C. cactorum* in the east, *M. prodenialis* tend to infest plants with higher crude fiber content than *C. cactorum*. Tissue crude fiber content may thus play an important role in both constraining infestation of host plants by *C. cactorum* in its current invasive range as well as determining its future spread in North America.

1. Introduction

A multitude of hypotheses have been posed to explain the success of biological invasions. Catford et al. (2009) provide an important synthesis, defining three broad classes of hypotheses for invasion success: effects based on propagule pressure of the introduction(s), effects based on abiotic tolerance limits of the invader, and effects based on the acquisition of novel biotic interactions, or the loss of interactions in the invaded community. Once a species has been introduced, abiotic conditions and biotic interactions act as a series of filters that constrain invader establishment and spread at multiple spatiotemporal scales (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; MacArthur, 1958; Chase and Leibold, 2003; Catford and Jansson, 2014). In landscapes that satisfy the invader's tolerances (e.g., thermal balance and water balance), persistence and spread of the invader will invariably depend on the set of interactions it develops with members of the native communities (Torchin et al., 2003; Colautti et al., 2004; Jiménez-Valverde and Peterson, 2011). The success of biological invasions can thus be affected by the set of traits possessed by the invader and those present in the community being invaded.

Any biotic interaction in a community arises from the set of functional traits possessed by the individuals involved, relative to the environmental context. Consequently, the traits possessed by an invader, and those possessed by species in the native community into which it was introduced, mediate the interactions that influence the invader's persistence (Sih et al., 2010; Guisan et al., 2014; Tingley et al., 2014). One of the earliest hypotheses of how biotic interactions might influence invasion success is the naturalization hypothesis (Darwin, 1859). The naturalization hypothesis proposes that close, common ancestry between an invader and a native member of an invaded community results in considerable overlap in the functional traits of the species. This overlap in functional traits can increase the likelihood of antagonistic interactions (from competition to parasitism) between the species (Lavorel and Garnier, 2002; McGill et al., 2006), and thus affect invader establishment and persistence in the invaded community (Daehler, 2001; Shea and Chesson, 2002; Agrawal and Kotanen, 2003; Mitchell et al., 2006; Jiang et al., 2010).

The successful establishment and spread of invasive species, particularly those with some degree of host specialization, is predicated on finding suitable food sources in the novel landscape. While the lack of a long co-evolutionary history with native species in invaded communities may

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allow the invader to circumvent the defenses of native species (Woodard et al., 2012), the availability of nutritionally suitable food is still necessary for establishment. These interactions are difficult to predict using geolocation of persistent populations in the invader's native range and extrapolating them based on some set of environmental predictors. Environmental suitability models (ESM) for exotic species that rely on strong interspecific interactions (e.g., specialized herbivores) reflect a complex interaction between a species' abiotic tolerances and the availability of suitable food in the native range (Brooks et al., 2012). Thus, without study of the nutritional requirements of the invader, ESM techniques can be misapplied and often fail to predict the occurrence and persistence of the invader in the exotic range (Werner and Peacor, 2003; Stang et al., 2006; Brooks et al., 2012; Verberk et al., 2013; Leach et al., 2015).

We argue that escaped biological control species provide an ideal opportunity to study the role of biotic interactions in determining invasion success. This is because the occurrence and persistence of biological control species is likely influenced by few, obligate associations with hosts or resources. Here we focus on the invasion by the South American Cactus Moth (*Cactoblastis cactorum* [Lepidoptera: Pyralidae]) of North American prickly-pear (Tribe Opuntieae). The study and rearing of *C. cactorum* as a biological control on prickly-pear in Australia, South Africa, and the Caribbean (among others) during the early 20th century produced extensive life history information and ecology for this species (Dodd, 1940; Pettey, 1948; Simmonds and Bennett, 1966). These moths are oligophagous herbivores that feed only on prickly-pear cactus species in Tribe Opuntieae. There are relatively few other herbivores that also feed on the stem segments of prickly-pear cacti; most of these are sap feeders (*Chelinidea* spp. and *Dactylopius* spp.), cactus weevils (*Gerstaeckeria* spp.), and other cactus-feeding moths (Johnston and Tryon, 1914). There also are other consumers that feed on prickly-pear flowers and fruits, or that colonize rotting tissue (Johnston and Tryon, 1914), but the community of species (excluding microbes) that could directly interact with *C. cactorum* is relatively simple.

Introduction of *C. cactorum* into North America likely occurred from Caribbean biocontrol populations as early as the 1980's (Habeck and Bennett, 1990; Dickel, 1991). Recent studies suggest that there have been three introductions into Florida (Simonsen et al., 2008; Marsico et al., 2011). The moth has since spread north along the Atlantic coast to Charleston, South Carolina (Hight et al., 2002) where the northern limit of the invader has remained constant for almost 15 years. Along the Gulf coast, *C. cactorum* has spread west to its current western range limit in the parishes southwest of New Orleans, Louisiana (Rose, 2009) (see Dodd (1940), and Zimmermann et al. (2004) for additional details on *C. cactorum* life history). Field studies suggest that the identity and availability of *Opuntia* hosts appear to influence both the native and exotic geographic distribution of the moth (Brooks et al., 2012, 2014; Sauby et al., 2012). Adult moths do not feed, so field observations concerning host use may reflect differences in larval survivorship on different hosts (Awmack and Leather, 2002). Hatched larvae generally do not leave the host plant onto which they are placed, so cactus moths are almost invariably provided one source of food (and thus one ratio of macronutrients, termed a rail) on which to develop. Based on the natural history of *C. cactorum*, we might expect to find larvae infesting more plants whose macronutrient content is close to the optimal intake rails than those whose tissues are more different (whether because ovipositing females can detect this, or because larvae will be more likely to survive and thus be more likely to be sampled).

We organize the present study around two interactions that could influence local success and the future spread of *C. cactorum* in North America: nutritional suitability of hosts, and potential competition for hosts with a native cactus moth, *Melitara prodenialis* (Walker). In particular, we ask:

- Can we describe a nutritional niche for *C. cactorum* by comparing infested and uninfested plants in its current, North American exotic range?
- Is it likely that native cactus moths (*Melitara prodenialis*) compete with *C. cactorum* for the same host plants?
- Can we determine the role that macronutrients may play in any future spread in North America?

2. Materials and methods

2.1. Study area and cladode sampling procedures

Collections of *Opuntia* stem segments (called cladodes) were made in two regions between May 2012 and March 2014. Within the range of *C. cactorum*, we collected 245 samples from 124 plants at 35 sites, 28 of these at the northern range limit of the herbivore along the Atlantic coast of South Carolina (Fig. 1). Additional sites in the range of *C. cactorum* were chosen to include inland sites in South Carolina, and an important endemic (*O. austrina*, ammophila entity) from Florida. We also collected from the region west of the current range of *C. cactorum*, taking 440 samples from 223 plants across 45 sites in Texas, New Mexico and Arizona (Fig. 1). Sites, and samples taken from these sites, are subsequently referred to as “eastern” if located in or east of Louisiana and “western” if located in or west of Texas.

A time-constrained search of 1 person-hour was conducted at each site in order to detect cactus moth infestation. During this search, cladodes with suspected cactus moth infestation (e.g., presence of an empty eggstick, frass, etc.) were quickly removed from the plant and set aside for further inspection. Following the time-constrained inspections, potentially infested cladodes were dissected to confirm infestation status. Any *C. cactorum* or *M. prodenialis* found were collected in glass scintillation vials and preserved in 90% ethanol. Undamaged cladodes were then also collected from both infested and uninfested plants for laboratory analysis of tissue macronutrient content. Collected cladodes were stored fresh in paper bags and kept inside large, plastic containers held at room temperature. For larger-statured *Opuntia*, at least 2 terminal cladodes were collected from each plant sampled. For smaller-statured *Opuntia* (i.e., *O. drummondii*), the entire above-ground plant was collected to obtain a sufficient sample of plant tissue for nutrient analyses. At least one of each species (as determined by field identification) was sampled at each site such that the total number of cladodes collected varied among sites. The GPS location for each sample collection was recorded along with information on host *Opuntia* height and growth form.

2.2. Quantifying Opuntia macronutrient content

All plants were identified to the lowest taxonomic level possible using Majure et al. (2012) and Majure et al. (2017) for eastern species, and Powell and Weedin (2004), and Powell et al. (2008) for those in the west. To confirm field identification, photos of each collection were made (minimum 8-megapixel resolution). Proximate analysis was used to quantify percent by dry weight of crude fiber, crude protein, and lipid in chlorenchyma, vascular tissue and medullar parenchyma from a subset of the plants collected in each region (38 in the current North American range of *C. cactorum*, and 37 across Texas, New Mexico, and Arizona). Samples for macronutrient analysis were chosen to provide replicate data for each common host taxon, for infested and uninfested plants, and to sample broadly across habitats. The time between fresh collection and tissue analysis varied among cladodes (but never exceeded 14 days), so tissues were removed immediately and in order of cladode collection after returning to the lab. All removed tissues were flash-frozen at −80 °C before freeze-drying at −45 °C and 133×10^{-3} mbar Torr until sample mass was constant. Procedural guidelines from the Association of Official Analytic Chemists (AOAC; Official Methods AOAC, 2012) were followed to quantify the crude fiber, lipid, and crude protein content of these freeze-dried tissues. Crude fiber was measured by H_2SO_4 and NaOH extraction, % lipid was measured by petroleum ether extraction, and % crude protein was measured via nitrogen analysis.