

Native ecotypic variation and the role of host identity in the spread of an invasive herbivore, *Cactoblastis cactorum*

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Abstract. Environmental niche models (ENMs) have gained enormous popularity as tools to investigate potential changes in species distributions resulting from climate change and species introductions. Despite recognition that species interactions can influence the dynamics of invasion spread, most implementations of ENMs focus on abiotic factors as the sole predictors of potential range limits. Implicit in this approach is the assumption that biotic interactions are relatively unimportant, either because of scaling issues, or because fundamental and realized niches are equivalent in a species' native range. When species are introduced into exotic landscapes, changes in biotic interactions relative to the native range can lead to occupation of different regions of niche space and apparent shifts in physiological tolerances. We use an escaped biological control organism, *Cactoblastis cactorum* (Berg.), to assess the role of the environmental envelope as compared with patterns of host–herbivore associations based on collections made in the native range. Because all nonnative populations are derived from a single *C. cactorum* ecotype, we hypothesize that biotic interactions associated with this ecotype are driving the species' invasion dynamics. Environmental niche models constructed from known native populations perform poorly in predicting nonnative distributions of this species, except where there is an overlap in niche space. In contrast, genetic isolation in the native range is concordant with the observed pattern of host use, and strong host association has been noted in nonnative landscapes. Our results support the hypothesis that the apparent shift in niche space from the native to the exotic ranges results from a shift in biotic interactions, and demonstrate the importance of considering biotic interactions in assessing the risk of future spread for species whose native range is highly constrained by biotic interactions.

Key words: *Argentina*; *Cactoblastis cactorum*; *ecotype*; *Florida, USA*; *invasive species*; *niche modeling*; *Opuntia spp.*; *plant–insect interactions*.

INTRODUCTION

In the half-century since Elton's classic treatise (Elton 1958), much of what we know about establishment of invasive species involves studies of small-scale patterns of interaction among species (Fridley et al. 2007) and investigations into the role of environmental heterogeneity at slightly larger scales (Fridley et al. 2007, Stohlgren et al. 2008). At much larger spatial scales, i.e., regional to continental, the focus shifts to the physiological limitations of the invader and how those establish geographic limits to invasion (Soberón and Peterson 2005). While the manner in which biotic interactions influence large-scale rates and routes of invasion are increasingly well studied for nonnative plants (Mitchell et al. 2006), their role in animal invasions is much less well studied.

Despite recognition of the potential importance of biotic regulation in the dynamics of invasion spread

(Mitchell et al. 2006, Sih et al. 2010), most attempts to predict the range extent of an invader have focused on abiotic factors alone, largely through the lens of environmental niche models (ENMs). There has been a recent explosion in the use of ENMs due to increasingly affordable computing power, the availability of large-scale data through remote sensing, and the myriad software packages available to estimate habitat quality in space. This approach implicitly assumes that species interactions are unimportant to determining the distribution of exotic species.

A number of authors have discussed the potential importance of considering biological interactions in environmental niche models (e.g., Guisan and Zimmermann 2000, Soberón and Peterson 2005, Heikkinen et al. 2007, Soberón and Nakamura 2009), but there has been no consensus over when such factors are likely to be important. Soberón (2010) argues that this may be an issue of scaling and that the influence of biotic interactions may be influential at local scales only. However, we argue that the importance of incorporating biological interactions when extrapolating niche predic-

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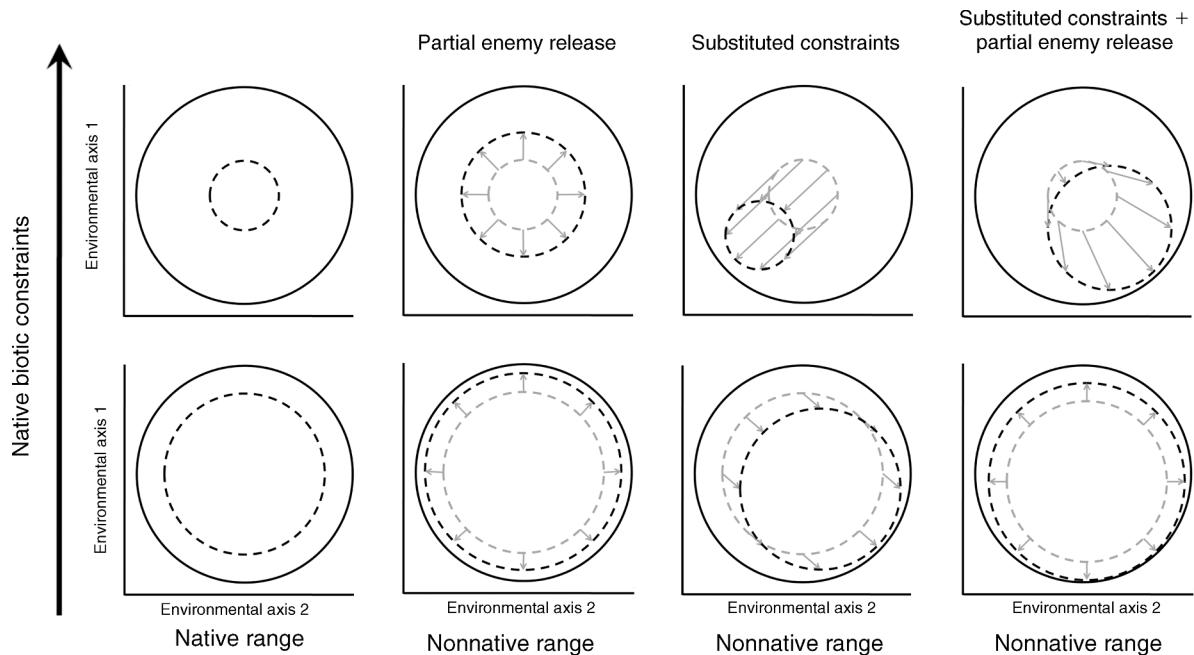


FIG. 1. Diagrammatic representation of the ecological explanations for an apparent niche shift. The realized niche (dashed black circles) is nested within the fundamental niche (solid black circles) in each. Arrows show the direction of change between the realized niche in the native range (gray dashed circles) and the realized niche in the exotic ranges. The predictive power of niche models developed from observations in the native range and applied to the exotic range should be proportional to the area of intersection between the two broken circles.

tions at large spatial scales is directly related to the relative size of the realized vs. the fundamental niche in the native range. Strong biotic constraints on the distribution of a species in its native range (e.g., for specialist consumers) can greatly reduce the size of the realized niche relative to physiological limitations (Fig. 1, top row). Likewise, ecotypic variation in biotic interactions may produce a similar effect when genetic isolation allows for local adaptation with interacting species while environmental tolerances are relatively homogeneous across the species' range. In either case, the large difference between the realized and fundamental niche in the native range can lead to a shift in occupied niche space after invasion. This is particularly true when the invading propagules represent a subset of native genotypes or ecotypes present in the exotic range of a successful invader. Thus, genotypic or ecotypic subsampling can provide one explanation for poor fit of ENMs between a species' native and exotic ranges (Randin et al. 2006).

Changes in the identity of interacting species, e.g., due to substitution of exotic for native constraints, is another mechanism that can lead to a shift in occupied niche space, absent any shifts in the species' fundamental niche (i.e., without any evolutionary change in the physiological tolerances of the invader). For example, release from natural enemies can lead to an expansion of the occupied region of fundamental niche space (Fig. 1, second column), while a substitution of the species

involved in particular roles (i.e., novel herbivores, predators, prey, etc.) can lead to an ecologically driven shift in occupied space (Fig. 1, third column).

Biotic substitutions in the patterns of species interactions are likely to occur with many invasions. While there is an expected loss of ecological connections as a function of introduction into novel ranges (Torchin et al. 2003), many exotic species acquire novel enemies and/or hosts in the exotic range. For example, the invasive herbivore *Xyleborus glabratus* Eichhoff (redbay ambrosia beetle) has infested six novel host species across four plant families in the eastern United States, potentially in a span of ~10 years (Koch and Smith 2008). Over a similar period, *Agrilus planipennis* Fairmaire (emerald ash borer) has been documented to infest three species of *Fraxinus* (ash tree species) in the Midwestern United States (Poland and McCullough 2006). These novel interactions that arise, whether the result of ecological or of evolutionary shifts, can have important effects on the dynamics of invasion (Sih et al. 2010) that may ultimately alter the region of the fundamental niche that is occupied in the exotic range relative to the native range (Fig. 1).

Exotic consumer species, such as escaped biological control organisms, provide ideal study systems to assess both abiotic and biotic constraints on invasion. Each biocontrol agent is introduced to regulate a particular host or prey item, and escape in the introduced range is the direct consequence of the ability (whether existing or

evolved) to use alternative hosts. Additionally, there is usually extensive knowledge of the natural history of the organism and of the specific collections and introductions that have occurred.

These are all true of *Cactoblastis cactorum* (Berg) (South American cactus moth) which is widely known as one of the most successful biocontrol organisms ever used. Immediately following the end of British rule in Australia, the spread of nonnative prickly pear (genus *Opuntia*) had rendered millions of hectares of grazing lands unusable (Dodd 1927, 1940). This prompted the establishment of the Prickly Pear Travelling Commission (Johnston and Tryon 1914) and the Prickly Pear Board (Dodd 1927) who were charged with finding economic uses and natural enemies of *Opuntia* that could help to reclaim the overrun pasturelands. Alan Dodd (1927, 1940) collected larvae of *C. cactorum* from *Opuntia elata* var. *cardiosperma* and another related species (likely *O. elata* var. *elata* or *O. megapotamica*) near Concordia, Argentina, in January 1925. These larvae were reared and mated in Argentina, and ~2750 eggs were transported to Australia. Approximately 3 billion eggs were subsequently spread across Queensland and New South Wales, resulting in the reclamation of millions of hectares of rangeland that had been previously overrun with *Opuntia stricta* and other *Opuntia* species (none of which are native to the region from which the moth was collected) (Dodd 1940). Subsequent introductions were made from Australia into South Africa (18 000 eggs in December 1932; Pettey 1947) and from South Africa into the West Indies (100 larvae and 300 eggs in March 1956; Simmonds and Bennett 1966). It is apparently the intentional introduction into the Caribbean region and subsequent spread of the moth that led to its unintentional introduction into south Florida, USA, sometime prior to 1989 (Marsico et al. 2011).

Patterns of strong host association for *C. cactorum* in exotic landscapes have been previously suggested by other authors (e.g., Dodd 1940, Pettey 1947), but only McFayden (1985) has made an attempt to identify geographic patterns of host use and morphology in the moth's native range. The concordance between McFayden's biotype map and the pattern of *C. cactorum* genetic structure in the native range (Marsico et al. 2011) suggests the potential that these groups represent ecotypes within the species. As a result, we hypothesized that biological interactions are likely to have played an important role in the global spread of *C. cactorum*. In particular, we hypothesized that the export of a single ecotype of the moth has imposed (and will continue to impose) strong biotic constraints on the exotic distribution of *C. cactorum*. Under this hypothesis we expect that niche models based solely on abiotic conditions at locations of observed presence will correctly predict the distribution of *C. cactorum* in nonnative landscapes only where there is a large overlap between the realized niches in the exotic and native ranges.

MATERIALS AND METHODS

Study system

Larvae of the South American cactus moth, *Cactoblastis cactorum* (Berg) feed gregariously inside the stem segments (cladodes) of infested cacti and can, in sufficiently large numbers, kill the host plant. Individuals pass through five to six larval instars before emerging from the plant to pupate, typically at the base of the infested plant. Adults emerge and will usually mate and lay eggs locally when host density is high, though they are capable of moving distances of at least 24 km between patches (Dodd 1940). Once mated, females deposit eggs in linear chains of 80–100 eggs (termed "eggsticks"), attached to the surface of cladodes (Neunzig 1997). A minimum of eight neonate larvae are then required to penetrate the cuticle and epidermis of the plant (L. Varone, G. A. Logarzo, and M. Manteca-Acosta, *unpublished manuscript*). Additional information on the natural history of the moth can be found in Dodd (1940), Pettey (1947), Mann (1969), and Zimmermann et al. (2004).

Field collection

We conducted thorough searches of *Opuntia* spp. across 12 Argentinean provinces (Buenos Aires, Entre Ríos, Corrientes, Santa Fe, Chaco, Córdoba, Santiago del Estero, Salta, Jujuy, Tucumán, Catamarca, and La Rioja) in February and December 2008 (sampling sites shown in Fig. 2). An effort was made to sample across a broad range of environmental conditions under which *C. cactorum* can be found. The question of how many species of *Cactoblastis* exist in the region is an area of active investigation (P. Zamudio [Universidad Nacional de Tucumán], *personal communication*). As a result, we took care to develop a sampling regime that would extend beyond the boundaries of the eastern group identified by Marsico et al. (2011) and that would represent the core of the species' native range, which extends into southern Paraguay, Brazil, and western Uruguay (McFayden 1985). Collection sites were identified using previously published locales for *Opuntia* hosts and the knowledge of plant locations by G. A. Logarzo and L. Varone (*personal observations*). Sample sites ranged from *Opuntia* plantations in which monocultures existed to more diverse assemblages occurring along roadsides and in natural areas. Exhaustive searches were conducted in each site and on all *Opuntia* species present in an effort to detect eggsticks, larva, and pupae resulting in an assemblage of 145 sites–host plants (there were 105 independent locations, and 31 locations had more than one species present for 145 site–host combinations). When damaged cladodes were located, we cut the stem segments open to determine whether larvae were present. Eggsticks were collected and transported back to the U. S. Department of Agriculture–Agricultural Research Service (USDA–ARS) South American Biological Control Laboratory (SABCL) in

Buenos Aires, Argentina, where resulting larvae were reared to late instar stages. Preserved larvae were utilized for genotyping by sequencing an 875bp region of the mitochondrial cytochrome oxidase I (mtCOI) gene to confirm mtCOI haplotype and haplotype group (see Marsico et al. [2011] for sequencing details). Vouchers of host plants are deposited in the plant collection of the SABCL. Fabián Font, a botanist at the University of Buenos Aires, Argentina identified the *Opuntia* species.

Habitat and niche modeling

We constructed several different habitat maps using the MaxEnt algorithm (Phillips et al. 2006) to predict habitat using 5 BIOCLIM variables (Hijmans et al. 2005) that we hypothesized to be important for *C. cactorum* or its potential hosts. We began by selecting 12 potential predictors and selected the final five (maximum temperature of the warmest month, mean temperature of the warmest and coldest quarters, and precipitation in the driest month and wettest quarter) by eliminating variables in the original set of 12 predictors for which we found significant covariation ($r^2 > 0.70$). We resampled these BIOCLIM layers to a 3-km raster in order to reduce computational time in constructing the models. The first group of models was based on 50 native collection sites (some with more than one host species present), including a model in which habitat was defined by all presence points, and four that used only points from one of the four phylogroups defined by Marsico et al. (2011). We considered a number of potential approaches to determining an appropriate cutoff value from MaxEnt's logistic output to distinguish habitat from non-habitat. We used the lowest presence threshold as described by Pearson et al. (2007) as a baseline threshold because it represents the highest value at which all native locations are defined as habitat. Likewise, for the minimum probability of presence for a site to be considered "habitat" we used cutoffs of 0.5 and the 25th percentile for MaxEnt's prediction for comparison. Because we were interested in the ability to accurately model exotic habitat using native presence data, we evaluated model quality as the ability of each model to predict *C. cactorum* presence for known collection locations in eastern Australia and Florida.

In order to assess the degree to which the introductions of *C. cactorum* into Australia and Florida represented a substitution of constraints via introduction, we randomly sampled the conditions (as defined by the habitat variables used in the MaxEnt models) at 29 505 sites across the known distribution of the moth in North America, South Africa, and Australia, and across the predicted distribution (based on habitat maps) in South America. All points were at least 3 km apart (the grain of our resampled environmental data). The total number of samples in each area ranged from 20 064 points across the native range in South America (Argentina, Uruguay, Brazil, Paraguay, Bolivia, and

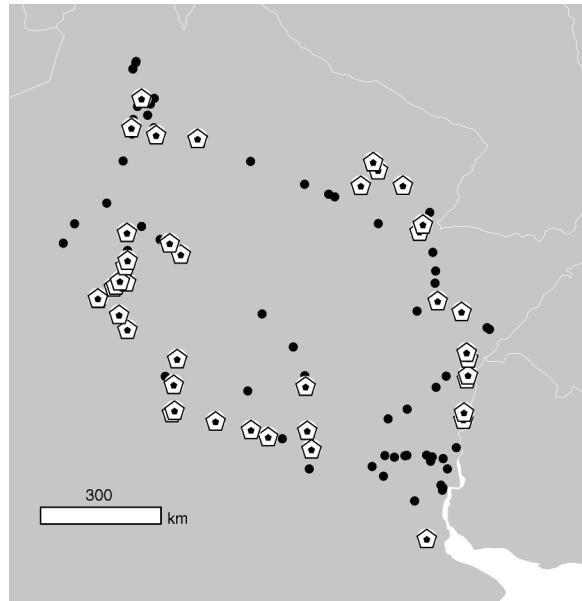


FIG. 2. Presence locations (white pentagons with internal black pentagons) used in the modeling of *Cactoblastis cactorum* habitat, and sampled sites where *C. cactorum* was absent (solid black circles).

Chile), to 4093 sites across the infested area of Florida, Alabama, Mississippi and Louisiana, to 5348 sites within the area of eastern Australia in which *C. cactorum* was released to control *Opuntia* infestation (Dodd 1927). This sampling density was chosen in order to sample 80% or more of the pixels in the defined regions. Principal-components analysis (PCA) was then used to generate composite variables defining the available environmental envelope in all regions. This allowed us to reproduce Fig. 1 from our data and to assess the location of each native collection site described in Marsico et al. (2011).

Host-plant associations

The association between host species and the genetic group of the larvae infesting each plant in the native range was determined by constructing a contingency table in which rows represented the previously identified ecotypes from Marsico et al. (2011) and columns correspond to the most common host taxa across the native range. A Fisher exact test was used to assess whether any association between ecotype and host species existed across the region. All statistical analyses were conducted using the R statistical language (R Core Development Group 2010).

RESULTS

Searches resulted in the detection of *Cactoblastis cactorum* eggs, larvae, or pupae in 50 of 105 locations sampled across the native range (47.6% of locations, 58/145 (40%) of sites–host plants). Habitat models constructed based on these native sampling locations

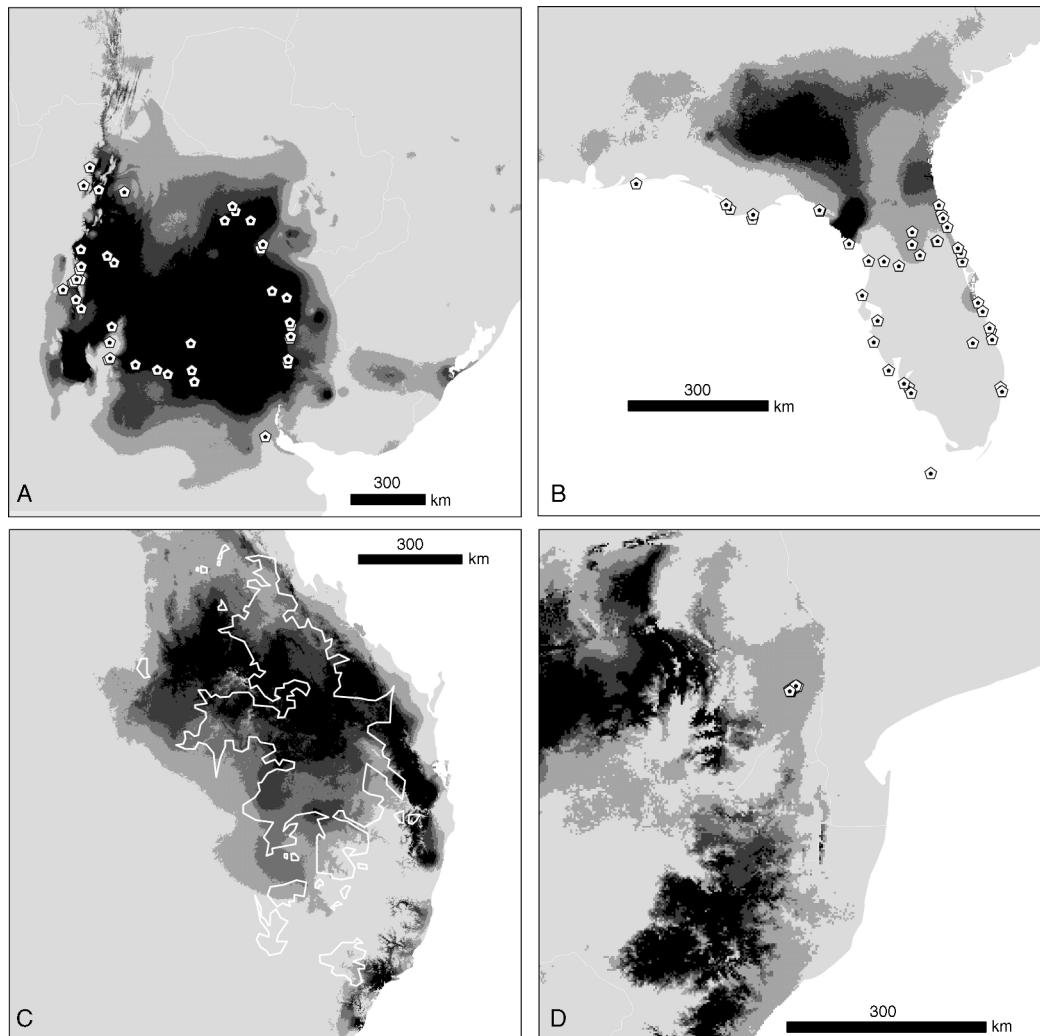


FIG. 3. Models of *Cactoblastis cactorum* habitat fitted using native points as training data: (A) The native range in South America, specifically, Argentina, Uruguay, Paraguay, Brazil, and a bit of Bolivia; (B) Florida, USA; (C) Australia's eastern region; (D) South Africa. Darker grays indicate a higher threshold for defining habitat (habitat-use probabilities, respectively for panels A–D, were 0.33, 0.50, 0.58, and 0.66 [from the MaxEnt algorithm; Phillips et al. 2006]). The white outlines in the lower left panel show the extent of moderate and heavy *Opuntia* infestation as mapped by Dodd (1927).

provided an excellent prediction of habitat within the native range. The specific percentage of true positives ranged from 100% for the lowest presence threshold for assigning “habitat” to 73.9% for the 25th percentile cutoff for habitat. The models were ineffective at predicting the contemporary distribution of the moth across all nonnative landscapes, irrespective of the cutoff used (Fig. 3). The proportion of correctly predicted presence points was significantly lower for all exotic landscapes when compared with those in the native range (binomial generalized linear model, $P < 0.001$), irrespective of the cutoff value used. The model constructed using the same geographic region as Dodd's (1927, 1940) original collection (the eastern phylogroup in Marsico et al. 2011) were similarly poor predictors of

exotic habitat, predicting 0% of the contemporary presence locations in Australia and the United States (model not shown). A comparison of the native model's prediction of habitat to Dodd's map of *Opuntia* infestation (Dodd 1927) does, however, show that almost all of the region identified in Dodd's map lies within predicted habitat area for both the lowest presence threshold and the 0.5 cutoff for habitat (Fig. 3).

In order to assess the degree to which environmental conditions across native and exotic landscape were similar (i.e., to reproduce Fig. 1 for this example), we examined PCA plots for the five predictor variables used in our habitat modeling exercise (Fig. 4). Plots of the native collections onto a plot of the top two PCA axes (77.7% of total variation accounted for by these axes)

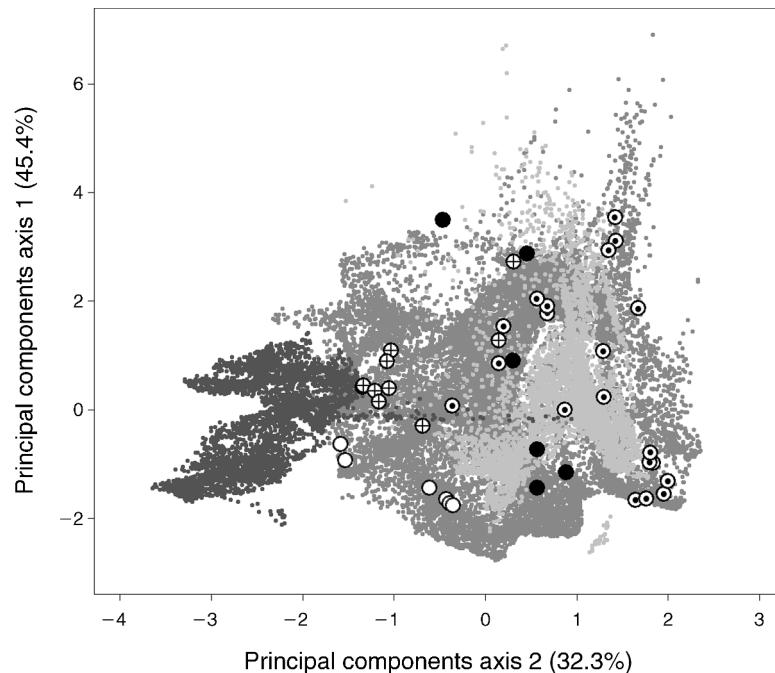


FIG. 4. The environmental envelope available in the native range (medium gray dots), the invaded region of eastern Australia (light gray dots), and the invaded region of North America (dark gray dots). Circles indicate collections from the eastern (white with a black cross), northeastern (open white), northwestern (solid black), and western (white with a black dot) phylogroups as defined by Marsico et al. (2011).

reveal that the environmental conditions within the area where Dodd and colleagues released the original introduced population of *C. cactorum* in Australia (light gray dots) are similar to conditions found in the native range (medium gray dots). In contrast, there is much less similarity between the available environmental conditions in Florida (dark gray dots) compared with those observed in the native range or in Australia. Collections in the eastern phylogroup and the northeastern phylogroup experience conditions that are intermediate to those found most frequently in Australia and Florida.

We then examined patterns of host association between each of the four genetic groups defined by Marsico et al. (2011) and different species of host (Table 1) in order to determine whether or not the patterns of

host use observed in the field were concordant with previously determined genetic structure. Analysis suggests that there was an overrepresentation (positive association) between the native host *Opuntia cardiosperma* among larvae from the eastern and northeastern groups combined ($P = 0.0188$). The nonnative host species *O. ficus-indica* is overrepresented among larvae from the west and northwest groups ($P < 0.001$, $P = 0.0129$, respectively). While the statistical association reveals a significant bias, it is impossible to distinguish an association due to regional relative availability of particular host species from any other explanation. It should be emphasized that our goal here is not to establish a preference for the moths within regions, but simply to demonstrate that regional patterns of bias are

TABLE 1. Table showing the pattern of host (prickly pear, *Opuntia*) attacks across phylogeographic regions defined by Marsico et al. (2011) in the native range of the South American cactus moth, *Cactoblastis cactorum*.

Region	<i>Opuntia</i> spp. (no. attacks)					Other spp.	Total no. of attacks
	<i>O. anacantha</i>	<i>O. e. var. cardiosperma</i>	<i>O. e. var. elata</i>	<i>O. ficus-indica</i>	<i>O. megapotamica</i>		
Northeastern	6 (37.5%)	6 (37.5%)	—	4 (25.0%)	—	—	16
Northwestern	—	—	—	16 (94.1%)	0 (0.0%)	1 (5.9%)	17
Eastern	0 (0.0%)	11 (39.3%)	13 (46.4%)	3 (10.7%)	0 (0.0%)	1 (3.6%)	28
Western	—	—	13 (8.6%)	116 (76.3%)	16 (10.5%)	—	152

Notes: Numbers in parentheses show the percentage of each host species infested across regions. Species that are not present in a particular region are denoted by dashes. Note that in the absence of reliable data on the relative abundance of hosts in each region it is impossible to quantify how much of the pattern is a function of host availability (i.e., relative abundance patterns across regions) and how much is a function of host preference.

concordant with previously observed patterns of larval morphology and genetic structure. Thus, our results may indicate local adaptation in the ability of this moth to develop on different host species, or they may reflect host-species turnover across regions due to environmental gradients, or some combination of these effects—an issue to which we will return below.

DISCUSSION

Our results suggest that invasion success for *Cactoblastis cactorum* is likely to have been governed, in large part, by the availability of suitable host plant species found in exotic landscapes, rather than by the moth's environmental tolerances. By plotting presence locations for the ecotype that was exported from the native range (white circles with black cross on Fig. 4) on the conditions found across the species' native range (medium gray dots on Fig. 4) it is clear that the realized niche for this eastern group (represented by "presence" points) is much smaller than the environmental envelope available in the native range. Furthermore, there is little overlap between the realized niche of this eastern group in the native vs. the exotic ranges (light and dark gray dots on Fig. 4), and so it is not surprising that the extrapolation of environmental conditions from the native range of *C. cactorum* using environmental niche models (ENMs) is not a strategy that can accurately predict the moth's future distribution in nonnative landscapes. In fact, the environmental variation across the native range is less than the total environmental variation across locations with persistent populations in the native and exotic ranges combined (Fig. 4). There are two potential explanations for this: there has been rapid evolutionary change in the fundamental niche of exotic *C. cactorum* populations, or the realized niche space has shifted to a different region of fundamental niche space as a result of a novel suite of biotic constraints in the exotic range. There are several pieces of evidence that suggest that evolution of the fundamental niche is unlikely in this case and that the observed shifts in occupied niche space result from a substitution of biotic constraints.

Genetic diversity is limited for *C. cactorum* in the exotic range, with little divergence observed in comparison to the native range (Marsico et al. 2011). Low genetic diversity restricts opportunities for evolutionary change, especially over timeframes such as those associated with the *C. cactorum* invasion. The small sample collected by Dodd (~14 adult females based on the fecundity reported by Dodd [1940]) and subsequent "sampling" of the Australian collection into South Africa and the Caribbean has resulted in a low genetic diversity within exotic populations as compared with the native range (haplotype diversity in Florida was 13% of that found in the native range (Marsico et al. 2011) after approximately 60 generations in North America).

The more parsimonious explanation for the observed patterns is that the realized niche in the native range is

sufficiently small, relative to the whole of this species' fundamental niche, to allow for a shift and/or expansion of the realized niche in the landscapes where *C. cactorum* has been introduced. Our data suggest that association with specific host species may play an important role in determining invasion success, although we cannot rule out alternative biotic effects.

There is extensive evidence for differential infestation success of particular *C. cactorum* ecotypes on different species of *Opuntia* in the field. Unlike Dodd's collections in 1925–1926, larvae collected by Johnston and Tryon (1914) from a cactus garden in La Plata, Argentina, during 1912 were capable of feeding, but not pupating, on *Opuntia* from eastern Australia. Likewise, both Pettey (1947) and Dodd (1940) noted variable success on different species of *Opuntia* in South Africa and Australia, respectively. Surveys of natural populations of *C. cactorum* in Florida have identified a small number of species commonly infested by *C. cactorum* in the field (Sauby 2009, Baker and Stiling 2009), although laboratory feeding trials suggest a broader host range (e.g., Zimmerman et al. 2004). The juxtaposition of laboratory and field trials may suggest that host effects are indirect (sensu Robertson and Hoffmann 1989).

We expect that ecotypic variation in the native range will be reflected in exotic landscapes; that is, if ecotypes exist and differ in their host use across the native range we expect that exotic populations may also display strong host association, especially under field conditions (cf. Sauby 2009). Specific host-association patterns are apparent across the native range (Table 1), and there is some evidence (although not conclusive) that these patterns may reflect ecotypic variation. McFayden (1985) used larval morphology and host preference to identify several potential *C. cactorum* "biotypes" across South America. The spatial distribution of McFayden's biotypes, and the data on host use reported here also correspond with patterns of genetic structure in the native range (Marsico et al. 2011). Although with the current data we cannot separate host preference from host availability, the concordance of spatial patterns in genetic isolation and host association suggests local adaptation to available host species and points to a potential genetic basis for distinct ecotypes across the native range.

The consequence of differential infestation success would be that host community structure, particularly the presence or absence of influential host species (Sauby 2009), could largely dictate the potential risk of invasion. Without detailed knowledge of the relative abundance of different host species across the native range, it is impossible to demonstrate that the observed patterns reflect anything more than variation in host availability. However, we did observe increased infestation in sites containing *O. ficus-indica* in the western region of Argentina (data not shown), suggesting that at least this association may reflect preferential oviposition or survivorship at those sites. Ultimately, the implication of our

findings, regardless of the underlying mechanism, is that variation in the patterns of host–consumer interactions may influence the rates and routes of invasion to a greater degree than climatic restrictions in this species.

This is in agreement with the growing body of literature in which the acquisition of novel species interactions can alter the invasion dynamics for invasive herbivores (e.g., Mitchell et al. 2006). In particular, variation in the ability of hosts to defend themselves against herbivory may play a critical role in the success of invasive herbivores. Heterogeneity in host resistance has been shown to alter invasion dynamics in a number of other systems, including the balsam wooly adelgid (Witter and Ragenovich 1986), the invasive beech scale insect (Houston 1987), the hemlock wooly adelgid (Havill et al. 2006), and the emerald ash-borer (Rebek et al. 2008). In each system, the invasive herbivore was more successful where plant defenses were relatively weak (Gandhi and Herms 2010). Pathways associated with defense responses often are highly conserved in their recognition of an attack (Vance et al. 2009), and in the manifestation of defense responses (Howe and Jander 2008), suggesting that invasive herbivores and parasites may be more successful when attacking species that have naïve mechanisms of recognition and response. Similar responses have been hypothesized to occur in exotic predator–naïve prey associations (Sih et al. 2010), and even in North American *Opuntia* species, the host-plant responses to *C. cactorum* and the native *Melitara prodenialis* display such patterns (G. N. Ervin, unpublished data).

The concept that invasion dynamics are influenced by changes in the patterns of species interactions from an invader's native range to the exotic range is not novel. Yet, we are beginning to understand that the dynamics of invasion spread are often governed by the nature of shifts in the identity of interacting species. The present work is an effort to better understand the utility of ENMs as predictive tools and to expand on the conceptual foundation of the enemy-release hypothesis (Torchin et al. 2003, Colautti et al. 2004) and the novel-associations hypothesis (Callaway and Ridenour 2004, Colautti et al. 2004, Mitchell et al. 2006), and to highlight the role that shifts in host or prey community structure can play in determining the dynamics of invasion spread for consumers. It is likely that the success or failure of invasive consumers like *C. cactorum* may lie in the conservation and plasticity of host–consumer interactions (the realized niche), not just the conservation (or evolution) of the fundamental niche.

Finally, we emphasize that ENMs, like other statistical modeling approaches, represent hypotheses describing potential constraints on a species' distribution. The predictive power of these models for species invasions is then a direct result of the degree to which the hypothesis (the suite of predictor variables) is an accurate representation of the factors limiting establishment and spread in the native range can be extrapolated

to the exotic range. As such, it is possible that there are alternative explanations for the observed lack of fit, such as the exclusion of an important predictor of habitat or a lurking biotic factor other than host identity for which we lack data. Experimentation will be necessary to rule out the latter possibility, but the exclusion of an important predictor seems unlikely given the high predictive power of the model across the native range. The present analysis shows that using ENMs as hypotheses rather than predictive tools can reveal key information about the process of invasion. A conserved set of abiotic constraints between the native and exotic ranges is the null hypothesis typically associated with ENMs. In the present case, our data suggest that this hypothesis may not apply when the realized niche in the native range is much smaller than the fundamental niche (i.e., when biotic regulation is strong).

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