The Relative Importance of Herbivory and Abiotic Conditions to Demographic Rates of two Species of *Opuntia* Cacti in Florida

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# Introduction

Predicting the impacts of herbivores can be difficult because plants can offset these impacts through compensatory (Lu and Ding 2012; Strauss and Agrawal 1999) or even overcompensatory growth (Agrawal 2000). The ability to compensate may depend on resource availability, and thus intraspecific density-dependence and interspecific competition (Wise and Abrahamson 2007). Determining herbivore impacts is further complicated by the fact that plants interact with multiple herbivores (Morris et al. 2007). For example, plant species can evolve to tolerate and/or defend against attacks by co-evolved herbivores (Johnson 2011). In fact, plants may defend more effectively against an invasive herbivore when in close proximity to plants that have been attacked by a native herbivore (e.g., Woodard, Ervin, and Marsico 2012), thus making the response to herbivores context-dependent.

On the other hand, the importance of understanding the link between plant population dynamics and environmental variability is increasingly recognized since patterns of temperature and rainfall are expected to change due to global climate change (Oppel et al. 2014, Teuling et al. (2010)). Recent studies have found that models of plant distributions and population dynamics are improved if climatic variability is included (N. E. Zimmermann et al. 2009; Estay et al. 2011; Moles et al. 2014). The effects of changes in mean environmental conditions can be ameliorated by the effects of environmental variability (Lawson et al. 2015). Additionally, interactions between temperature and precipitation can lead to impacts more severe than the impact of variability in temperature or precipitation alone. For example, Teuling et al. (2010) found that increased hot, dry conditions can lead to decreased plant cooling via evapotranspiration.

The effects of precipitation and temperature may also shift the outcomes of plant-herbivore interactions (Maron, Baer, and Angert 2014). For example, multiple studies have shown that plant mortality and loss of biomass to insect herbivores can be increased by warming during periods of drought (Carnicer et al. 2011; McDowell et al. 2011). Barton, Beckerman, and Schmitz (2009) found that while temperature and precipitation did not significantly affect plant productivity directly, temperature moderated the strength of top-down indirect effects on plants. In another study, herbivory was more strongly influenced by precipitation, and the ability of plants to effectively defend against herbivores increased with temperature (Rodríguez-Castañeda 2013).

Our objective was to quantify the relative importance of herbivory by native versus invasive insect herbivores in the demographic rates of two related plant species, given the context of climatic variability. Our study system consisted of two species of native prickly pear cacti (genus *Opuntia*) in Florida and their specialist insect herbivores: the invasive South American cactus moth, *Cactoblastis cactorum* (Berg.) (Lepidoptera: Pyralidae), and three native insect species: the bug *Chelinidea vittiger* McAtee (Hemiptera: Coreidae), the scale *Dactylopius* species (Hemiptera: Dactylopiidae), and the moth *Melitara prodenialis* Walker (Lepidoptera: Pyralidae) (Figure 1). All four insect species feed exclusively on *Opuntia* species. We used a five year observational study of plant growth, fecundity, and survival and cactus insect presence/absence to address the following questions:

1. Does insect herbivore presence negatively affect cactus size, sexual reproduction and survival?
2. If so, do these effects vary depending on whether the insect species is native or invasive?
3. Do effects of insect herbivory on cactus size and sexual reproduction vary depending on weather conditions?
4. Are the effects of herbivory and weather consistent across the two cactus species?
5. What is the relative importance of insect herbivory and weather?

Anecdotal evidence from Australia suggests that the invasive moth negatively impacts cactus populations (Dodd 1940) but studies in Florida and elsewhere have shown mixed results with respect to the impact of the invasive moth to cactus vital rates (Jezorek, Baker, and Stiling 2012; J. H. Hoffmann, Moran, and Zeller 1998). Additionally, little is known about the impact of the three native insect species on native *Opuntia*, and the relative importance of herbivory in comparison to abiotic factors like temperature and precipitation. Cacti are generally more sensitive to low rather than high temperatures and are tolerant of drought conditions (Nobel 2002), but it is unclear if these relationships are modified by the presence of insect herbivores. We hypothesized that the invasive moth would have a greater, negative impact on cactus demographic rates than native insects. Invasive moth larval development increases with temperature (J. C. Legaspi and Legaspi 2007), and thus if the insects respond more positively to temperature than the plants, herbivory may have a greater impact to vital rates at higher temperatures, and thus will manifest as an interaction between insect presence and temperature in our models.

To address these questions, we formulated statistical models assuming that variation in cactus relative growth rate and fecundity were functions of past plant size, weather variables, and/or insect presence/absence. We ranked competing models using the conditional form of the Akaike Information Criterion (cAIC; Müller et al. 2013; Vaida and Blanchard 2005) to test hypotheses about which factors best explained variation in our data. These hypotheses included predictions that the vital rate was explained by (1) an insect species, precipitation (P), or temperature (T) alone; (2) combinations of insect species, P, and T; (3) interactions among an insect species and P or T; (4) interactions among P and T; (5) pooled native insect presence/absence, invasive moth presence/absence, P, and/or T; and (6) plant size at time t, , alone. The best model(s) among the models tested identified a parsimonious set of the most important predictor variables to each modeled vital rate. We then qualitatively compared model results for the two cactus species. We also explored which factors were correlated with cactus survival.

# Methods

## Study System

*Opuntia humifusa* (Raf.) Raf. is widely distributed throughout the eastern United States, from as far north as Michigan south to Florida and as far west as Texas (Figure 1, Benson 1982). *Opuntia stricta* (Haw.) Haw. is limited to the southeastern United States, ranging from coastal eastern Texas to South Carolina, and the Caribbean (Figure 1, Benson 1982). *Opuntia humifusa* is a shorter species, usually only reaching 30-60 cm in height, and sometimes trailing along the ground (Benson 1982). In contrast, *O. stricta* (listed as “Threatened” in Florida, FDACS 2015), can grow as a large shrub up to two meters in height (Benson 1982).

The invasive moth, *C. cactorum*, is a celebrated biological control agent of invasive *Opuntia* (e.g., in Australia, Dodd 1940) but is invasive in the southeastern US (Figure 1; H. Zimmermann, Moran, and Hoffmann (2000)]. First detected in the Florida Keys in 1989 (Dickel 1991), it arrived in northeastern Florida by 2002 (Hight et al. 2002). *Opuntia stricta* has been found to be the most frequently infested by the invasive moth in Florida relative to other cactus species (Sauby et al. 2012).

The native moth, *M. prodenialis*, is found across the southeastern U.S. and shares similar life history traits with the invasive moth. Both species attach linear chains of 20 - 90 eggs to cactus segments and larvae feed on tissue by boring within segments. Adults of both species live approximately 7 - 10 days and do not feed (Dodd 1940; Pettey 1948). Both moths undergo 2 - 3 generations per year in Florida (Hight and Carpenter 2009; J. C. Legaspi, Baez, and Legaspi 2008) with the larval stage lasting several months (Dodd 1940; Pettey 1948).

The native cactus bug, *Chelinidea vittiger*, is a coreid bug that is native to and widespread throughout North America (Figure 1). Damage to the plant from feeding may cause the plant to take on a sickly yellow appearance and growth may be impeded (Hunter, Pratt, and Mitchell 1912). Adults are known to fly only infrequently, instead moving primarly by walking (Mann 1969). *Dactylopius* sp. is a scale insect that is covered by secreted waxy materials with a white fuzzy appearance and is most often found feeding on young cladodes and fruit (Figure 1; Dodd 1940). Larvae may disperse passively via wind currents, but soon after hatching females select a position for feeding, insert the proboscis into the plant, and remain stationary for the duration of the life. The females then begin to secrete a waxy covering for protection that gives them their white, fluffy appearance (Dodd 1940; Mann 1969).

## Sampling Data Collection

Prickly pear cacti were surveyed over five years (four times in 2009, twice a year from 2010 - 2013, and once in winter 2014) across six sites in the Florida panhandle (Figure 2). At the initiation of the study in Winter 2009, plants were marked and surveyed at regular intervals along one to two transects per site established within patches of cacti such that between 15 to 20 plants of each cactus species, if present, were surveyed per site (*O. humifusa*: 109 total; *O. stricta*: 54 total). For all transects, plants were only sampled if they were found within two meters of a transect. For transects in which plants were sampled at even intervals, if no plants could be located within two meters of the transect at the given interval, the next nearest individual within two meters of the transect was sampled.

Transect lengths differed among sites to account for variation in cactus patch size and density. Patches of *O. humifusa* were relatively large at Nokuse and Torreya State Park (TSP), and thus at each site plants were sampled at 5 m intervals along a 100 m transect. At Big Lagoon State Park (BLSP), patches of *O. humifusa* were smaller and plants were sampled at 5 m intervals along two 50 m transects. At Henderson Beach State Park (HBSP), *O. humifusa* plants were selected at shorter intervals along a 50 m transect. Because *O. stricta* plants are larger and the populations are patchier at HBSP and Mexico Beach (MB), the first 15 to 20 individuals of *O. stricta* that were encountered along a transect were sampled rather that a regular interval as at the other sites. Finally, at St. Andrews State Park (SASP), both *O. stricta* and the nearest *O. humifusa* were sampled at approximately 5 m intervals along a 100 m transect. Although a third cactus species, *O. pusilla*, was present at some sites, this species was not included in transects because it was less abundant and has not been found to be an important host species for the invasive moth, possibly due to its very small size (Sauby et al. 2012).

During each survey, we recorded size (maximum height, maximum width, and number of cladodes [segments]), fruit abundance, and the presence/absence of the four insect species for each marked cactus plant. We also noted if any plants died. At each site, for each plant that died or was not relocated, another plant was added to the set of plants to be surveyed.

We excluded surveys of eight plants from May 2011 onward from the analyses of plant size and reproduction because of biomass removal by the USDA (QUESTIONS FOR COATHORS: do we know this for sure or should we restate?). We also excluded all observations of these plants from our survival analyses.

We created four datasets from our survey data: one containing all survey dates for use in the analysis of relative growth rate (RGR), two datasets for the analyis of fecundity (one restricted to surveys in the spring or summer and the other restricted to surveys in the fall or winter), and one dataset for the analysis of cactus survival (summarizing whether plants were still alive at the end of the study period and whether they had ever been infested by the four insect species).

## Weather Data

We downloaded daily maximum and minimum temperature data (measured in Celsius) and daily total precipitation (measured in cm) from the National Oceanic and Atmosphere Administration National Climatic Data Center (Menne et al. 2015) for the period from January 2008 to January 2014. We preferentially used data from the weather stations closest to each of our sampling locations, and filled in missing values with data from the next closest weather station (range of the number of weather stations used per sampling location: 2 - 10; distance between weather station and sampling location: mean = 20.41 km, range = 1.08 – 50.15 km).

We derived 16 variables from the temperature and precipitation data that we hypothesized would capture the average of and variation in weather conditions. Precipitation variables included daily precipitation total (mean and standard deviation), percentage of days with rain, the number of consecutive days with rain (mean, maximum, and standard deviation), and the number of consecutive days without rain (mean, maximum, and standard deviation). Temperature variables included daily maximum temperature (mean and standard deviation), average degree-day, the percentage of days with the minimum temperature below 0 C, and the number of consecutive days with the minimum temperature below 0 C (mean, maximum, and standard deviation).

We specifically included average degree-day to account for the accumulation of thermal energy available for growth and reproduction (Cayton et al. 2015). Degree-day was calculated the using University of California Statewide Integrated Pest Management Program Degree Day calculator (FIX CITATION FORMAT, California Davis Statewide Integrated Pest Management Program [UCD IPM], n.d.). We used the sine-wave method (Baskerville and Emin 1969), which has been found to be superior to other degree-day calculation methods (Baskerville and Emin 1969; Roltsch et al. 1999). We based the lower threshold temperature for both *O. stricta* and *O. humifusa* on information available for *O. ficus-indica* (L.) Mill., a well-studied, agricultural species that has a northern range relatively similar to *O. stricta* (Benson 1982). Two metrics of cellular activity, acid accumulation and nightly net CO uptake, occur between 0 C and 35 C (Nobel and Hartsock 1984). Additionally, Nobel and De la Barrera (2003) found that cell damage in segments occurs starting at -6 C and cell damage in fruit and roots occurs at temperatures starting at -7 C. Thus, we imposed a 0 C lower temperature threshold and excluded an upper temperature threshold because *Opuntia* are highly heat tolerant and segment, root, and fruit cell damage begins to occur at temperatures above between 55 and 65 C (Nobel and De la Barrera 2003).

## Statistical Analysis

For weather variables, we used quantile-quantile plots with 95% confidence intervals (function "qqPlot" in the "car" package, Fox and Weisberg 2011) in R (R Core Team 2015) to diagnose non-normality; when necessary, the weather variables were transformed to obtain approximate normality. Additionally, due to high collinearity among some of the weather variables, we performed Principal Components Analyses (PCA; McCune, Grace, and Urban 2002) using SAS software (PROC FACTOR method=principal, SAS Institute Inc., Cary, NC, USA) to obtain independent weather metrics for use in modeling. We calculated separate PCAs for the two cactus species because they occurred at different sites and thus we relied on separate weather station data (with the exception of HBSP and SASP where both cactus species were found, Figure 2). For *O. humifusa*, we also calculated separate PCAs for each dataset (all surveys, winter, and spring), and weather type (temperature and precipitation). Because of limited fecundity data for *O. stricta*, we did not include temperature or precipitation information in the fecundity analyses. Thus we calculated temperature and precipitation PCAs for *O. stricta* for only the dataset containing all surveys. For each PCA, we retained and rotated the first two axes to improve interpretability of the axes (as long as the first two axes had eigenvalues > 1; mineigen=1 and rotate=Varimax options). The retained and rotated axes were included in the RGR and fecundity analyses as composite variables (Tables 2 and 3).

We used the number of cladodes at time () as our measurement of plant size. For the fecundity and RGR datasets, we rescaled by centering values on the mean and then dividing by two standard deviations (Gelman 2008; Schielzeth 2010) in R ("rescale" function in the "arm" package, Gelman et al. 2015; R Core Team 2015). We included the rescaled variable in all fecundity and RGR models.

### Relative Growth Rate

Using each consecutive pair of size observations per plant, we calculated the annual relative growth rate, , using a modification of the formula from Paine et al. (2012),

,

where is individual of cactus species , is the number of days between surveys, and is time.

We modeled using linear mixed models (Proc GLIMMIX, SAS 9.4). Our full models for each cactus species were of the general structure , where is the response variable, is a vector of fixed effects coefficients, is a design matrix, is a vector of random effects coefficients, and is the design matrix.

For *O. humifusa*, the component of the full model included

and for *O. stricta*

,

where and represent *O. humifusa* and *O. stricta*, respectively. P and T represent the set of precipitation and temperature PCA axes, respectively. For the random effects , we considered four variables in combination and alone: plant identity, location, year, and location within year.

For each cactus species, we compared a number of models by varying the random effects included in the full models to test whether the inclusion of random effects improved model fit. We evaluated the fit of the models using likelihood ratio tests based on the asymptotic Chi-square distribution (Proc GLIMMIX, COVTEST CL (TYPE=ESTIMATED) option, SAS 9.4). For *O. stricta* models, we included as a random effect location within year, indicating that observations at a location tended to be correlated within a year. For *O. humifusa* models, we included plant identity, indicating that observations among individual plants tended to be correlated, and location within year as random effects.

Next, we estimated candidate models for both cactus species by varying the fixed effects from the full models to evaluate our different biological hypotheses about factors that could affect RGR (Table 4). We ranked the candidate models using the conditional form of the Akaike Information Criterion (cAIC; Müller et al. (2013), Vaida and Blanchard (2005)). The cAIC penalizes the negative log-Likelihood of a given model by considering the effective degrees of freedom. This lies somewhere between and , where is the number of fixed effects and is the number of random effects (is this the same as ?). Using a conservative approach, in R (R Core Team 2015) we estimated the effective degrees of freedom as the number of parameters, treating random effects as fixed effects in the model (; Müller et al. 2013, Vaida and Blanchard (2005)). We favored models with the lowest cAIC, except in cases where the cAIC value of a model with an equal or smaller number of parameters was within 2 cAIC units of the highest ranked model. (The cAIC value corresponds to the number of cAIC units between a model and the model with the lowest cAIC.) This was due to the fact that 2 cAIC units corresponds to the penalty given per parameter or effective degree of freedom (Arnold 2010).

### Fruiting Probability and Abundance

*Opuntia* flower production is generally restricted to the spring and summer (Gimeno and Vilà 2002; Godínez-Álvarez, Valverde, and Ortega-Baes 2003) and fruit ripen in the late fall and winter (K. Sauby, unpublished data; C. Miller, personal communication, Reyes-Agüero, Aguirre, and Valiente-Banuet 2006). We performed two separate model selection procedures for each cactus species to determine if our results were robust to the timing of surveys: on our dataset restricted to spring surveys and to the dataset restricted to only winter surveys. Our spring observations best capture total plant reproductive effort as manifested by the number of flower buds, flowers, and new fruit produced. In contrast, our winter survey data more closely captures the realized fecundity per plant via sexual reproduction. Neither dataset perfectly captures the realized fecundity of the plants: plants may produce additional fruit between our spring and winter surveys and our winter surveys may also underestimate realized fecundity because the winter count of fruit is generally restricted to those that have ripened as well as to those that have not been lost to flower or fruit herbivory, and other causes of mortality.

For each dataset and cactus species, we used a hurdle model with random effects to explain variation in fruiting probability and abundance. In a hurdle model, we separately formulate a binomial model explaining observations that fall above or below a "hurdle" (in this case, the hurdle is the production of fruit) and a model, conditional of the presence of fruit, explaining abundance observations above the hurdle (Min and Agresti 2005; Mullahy 1986). We estimated the fruiting probability component using logistic regression (PROC GLIMMIX, dist=binary) (fruit abundance component: TO DO). First, as with our RGR analysis, for each cactus species and dataset we compared a number of models by varying the random effects to test whether the inclusion of random effects improved model fit. For *O. humifusa*, we included the full set of fixed effects in our models (the same fixed effects as in the RGR analyses). However, for *O. stricta*, due to a small number of plants that varied in fruit presence during the study period, we restricted our fixed effects to . After determining the appropriate random effects for inclusion in the models, for our *O. humifusa* datasets we estimated and ranked candidate models that differed in their fixed effects as in our RGR analyses. For the *O. stricta* spring dataset, we excluded random effects because they did not improve model fit (Table 4).

### Survival

Due to the small number of plants that died during the study period, we performed contingency table analyses using Fisher's Exact Test (Proc FREQ Fisher option, SAS 9.4). We tested whether mortality was more likely if a plant was every infested by a particular insect during the 5 year study period. We also tested whether smaller plants were more likely to die during the study period; we placed plants into one of two size categories based on the size threshold at which plants begin to produce fruit (TO DO).

# Results

*Opuntia humifusa* and *O. stricta* were found at 5 and 3 of the sites, respectively (Figure 2). The frequency of insect presence varied by cactus species (Figure 3). Many *O. humifusa* individuals were either infested multiple times during the study period by the native moth or never infested (Figure 4). In contrast, most *O. stricta* individuals were infested multiple times by the native bug and the invasive moth during the study period (Figure 5). Additionally, presence/absence was weakly correlated among the insect species (Table 1). Over the five year study, only the invasive moth and the native bug were common on *O. stricta* (found at least once on 70% and 83% of the 54 total plants, respectively); in contrast, the three native insects, the native bug, moth, and scale, were common on *O. humifusa* (found at least once on 80%, 65%, and 65% of the 109 total plants, respectively). The invasive moth was found on only 11 *O. humifusa* plants during the study period. Thus for *O. stricta* models, we restricted the insect predictor variables to invasive moth and native bug presence/absence and for *O. humifusa* models, we restricted them to the presence/absence of only the three native insect species.

The Florida Panhandle received below average rainfall during 2011 and above average rainfall in 2013 (NOAA NCEI 2015). Across the six panhandle Florida sites, annual precipitation averaged 173.62 cm (range: 150.08 - 203.68 cm), the mean monthly maximum temperature averaged 25.49 C (range: 14.04 - 34.68 C), and the mean monthly minimum temperature averaged 14.04 C (range: 1.03 - 24.53 C).

The interpretation of the precipitation PCAs was similar for both cactus species and datasets. The first PCA axis, P1, was positively correlated with rainfall and the second PCA axis, P2, was negatively correlated with rainfall (Table 2). For the RGR datasets for both cactus species, the first PCA axis of the temperature PCAs, T1, was negatively correlated with temperature and positively correlated with variation in temperature. For the spring and winter datasets for O. humifusa, T1 was also negatively correlated with temperature and positively correlated with variation in the maximum temperature. T2 was positively correlated with mean maximum temperature (Table 3).

Among the candidate RGR models evaluated, for both cactus species the best models indicated that RGR was negatively associated with (Table 4). For both cactus species, RGR also had a negative relationship with P1 and positive relationship with P2, indicating that RGR was negatively correlated with rainfall. The RGR of both cactus species was also positively associated with the T1 axis, indicating that RGR was negatively correlated with temperature and positively correlated with variation in temperature. The two cactus species differed in terms of the insect species that affected RGR: while no insect species was included in the best model of *O. humifusa* RGR, for *O. stricta* the presence of the invasive insect was negatively correlated with RGR (Table 4). Finally, neither of the best models supported the inclusion of interactions among weather variables nor among weather and insect presence.

For *O. humifusa*, two models predicting spring fruit presence and three models predicting winter fruit presence were retained as best models due to the fact that all were within 2 cAIC units of the highest ranked models. For models explaining the presence of fruit on *O. humifusa*, the best models for the two datasets varied in their inclusion of weather variables: the full set of weather axes were included in the best models predicting spring fruit presence but were excluded from the best models predicting fruit presence in the winter. One of the best models predicting fruit presence in the spring also included the full set of interactions among weather variables. The effect of precipitation on fruit presence in spring was unclear because the 95% confidence intervals overlapped with zero for both best models. Spring fruit presence was generally positively correlated with both temperature axes, indiciating that fruit presence was negatively correlated with temperature but positively correlated with variation in the maximum temperature (Table 4).

The best models explaining spring and winter *O. humifusa* fruit presence also varied in their inclusions of insects, from full exclusion of insect species (winter dataset) to inclusion of the full set of the three native insect species (spring dataset; Table 4).

Most *O. stricta* plants were never observed with fruit (36 and 38 plants, spring and winter datasets respectively, out of 54 plants) and only a small fraction of plants varied in terms of fruit presence during the study time period (6 and 7, spring and winter datasets, respectively). Thus we included only as a fixed effect in our model, which was positively associated with fruit production, consistent with our observations from the *O. humifusa* models (Table 4).

The overall mortality rate for our five-year study was 16.5% (18/109) and 10.9% (5/46) for *O. humifusa* and *O. stricta*, respectively. (TO DO: INCLUDE OTHER SURVIVAL RESULTS.)

# Discussion

Fecundity

* Differences between spring and winter dataset indicate that the timing of data collection is important

Insects

* next explore impact of weather to insect herbivores
* increasing vital rate variability in response to changes in climatic variability is predicted to have a more strong and negative effect on short-lived species (like insects) relative to longer-lived species (*Opuntia*; Morris et al. 2008)

We are missing information on clonal reproduction as well as recruitment (sexual and clonal)

* very little recruitment in *O. stricta* from aborted fruit (K. Sauby, unpublished data)
* X% of new *O. stricta* recruits results through clonal reproduction (K. Sauby, unpublished data from Atlantic Coast)
* we do not have information about relative importance of clonal reproduction in *O. humifusa*
* some populations rely predominantly on clonal reproduction (Del Carmen Mandujano et al. 1998)
* mode of reproduction may be sensitive to weather conditions; negative relationship between clonal reproduction and precipitation in contrast to positive relationship between precipitation and sexual reproduction in *O. rastrera*, found in semiarid regions in Mexico (Mandujano et al. 2001)

Insect Impact

* we’re not able to determine if differences in insect impact is due to purely numerical differences (e.g., if the invasive is more abundant)
* Measure relationship between insect abundance and impact; here we just use presence/absence - Population density modifies the ecological impacts of invasive species
* does climate affect how the insects affect the plants? Or do the insects affect how the climate affects the plant? Our analyses do not address this problem.
* We are not sure if an insect competitively excluded another (and thus not accounting for that interaction)

Survival

* Data limitation making inferences about survival difficult
* for many iteroparous plants, fitness is more strongly affected by differences in survival rather than fecundity (Crone 2001)

Population Model

* The next step is to extrapolate these effects to population dynamics
* In a recent review of 37 papers on rare and/or threatened plant populations, only 3 extrapolated effects of herbivores on population size or growth rate (reviewed in Ancheta and Heard 2011).
* must be cautious about assumptions, since impacts to vital rates do not necessarily translate to impacts to population growth (e.g., Louthan et al. 2013)
* How do I incorporate RGR into a population projection model? My current RGR formula indicates that the magnitude of the insect and weather effects are proportional to size, if interpreted literally

Problems with understanding relationship to weather

* " Note that PCA is sensitive to outliers (extreme values), transformations, missing data and assumes multi-normal distributions. In practice, the technique is relatively robust when used for description (as opposed to hypothesis testing) so long as the data are con- tinuous, not strongly skewed and without too many outliers. "(Dormann 2012)
* "The former methods are problem- atic in the context of climate-change because the latent variables, extracted from currently prevailing correlation patterns, cannot be used with diverging future patterns. " (Braunisch 2013)

Other

* may be local adaptation to environmental conditions that reduce the impact to vital rates
* strong relationship with size matches other studies (Keeler and Tenhumberg 2011)
* Panhandle behaves differently than other parts of Fl due to invasion history
* Another approach one could imagine: fit growth models by individual plants, von bertolanfi approach where you fit parameters and functional form for the plants, how are the parameters affected by the insects and weather?; think about including that figure.

# Figures

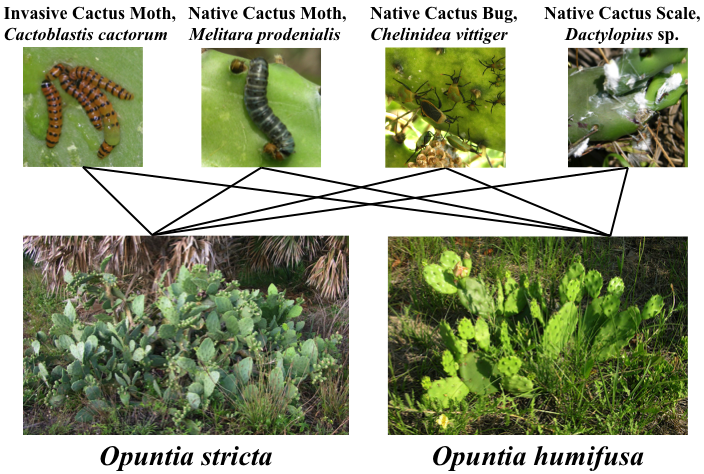


Figure 1. The two cactus species and four insect species found at the locations surveyed in the Florida panhandle. The lines connecting the insects and plants indicate that all insects have been found to feed on each of the cactus species.



Figure 2. Sampling locations in the Florida panhandle and the cactus species sampled there: *O. humifusa* (open squares) and *O. stricta* (solid squares).



Figure 3. Fraction of Total Number of Visits during the 5-year study period each insect species was found on each of the two cactus species. The upper and lower lines of the boxes correspond to the 25th and 75th percentiles while the horizontal line inside of the box corresponds to the 50th percentile. The vertical lines (“whiskers”) extend to 1.5 times the distance between the first and third quartiles. The points indicate values that lie beyond the whiskers.



Figure 4. Size measurements () for *O. humifusa* plants during the study period. Symbol shapes represent the presence/absence of the native moth.



Figure 5. Size measurements () for *O. stricta* plants during the study period. Symbol shapes represent the presence/absence of the native bug and invasive moth.

# Tables

Table 1. Factor loadings generated by Principal Components Analyses (PCA) of precipitation data for the three datasets for *O. humifusa* and for the RGR dataset (including all surveys) for *O. stricta.* The "P1" columns indicate the factor loadings from the first PCA axis and the "P2" columns the second PCA axis; the dataset used for the PCA is indicated in parentheses. Summary statistic abbreviations include maximum (Max.) and standard deviation (SD). Variables that were transformed prior to the PCA are indicated by the inclusion of the transformation in parentheses next to the factor loading score; transformations included the natural logarithm (log) and square root (sqrt)). All axes were rotated orthogonally to improve interpretability.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Variable | Summary Statistic | P1 (RGR) | P2 (RGR) | P1 (Spring) | P2 (Spring) | P1 (Winter) | P2 (Winter) | P1 (RGR) | P2 (RGR) |
| Species | Species | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. stricta | O. stricta |
| Daily Precipitation | Mean | 0.713 | -0.286 | 0.763 (log) | -0.185 (log) | 0.839 | -0.113 | 0.751 | -0.486 |
|  | SD | 0.556 | -0.03 | 0.589 | -0.052 | 0.74 | -0.126 | 0.642 | -0.338 |
| Percentage of Days with Rain |  | 0.718 (log) | -0.594 (log) | 0.705 (log) | -0.607 (log) | 0.769 (log) | -0.553 (log) | 0.78 | -0.562 |
| Number of Consecutive Days with Rain | Mean | 0.912 (log) | 0.036 (log) | 0.872 | 0.127 | 0.941 | -0.068 | 0.946 | 0.038 |
|  | Max. | 0.872 (log) | -0.179 (log) | 0.682 (log) | -0.246 (log) | 0.788 (log) | -0.17 (log) | 0.919 (log) | -0.101 (log) |
|  | SD | 0.917 (log) | -0.08 (log) | 0.86 (log) | 0.01 (log) | 0.883 (log) | -0.122 (log) | 0.959 (log) | -0.017 (log) |
| Number of Consecutive Days without Rain | Mean | -0.352 | 0.841 | -0.317 | 0.872 | -0.492 (log) | 0.781 (log) | -0.315 | 0.853 |
|  | Max. | 0.052 (log) | 0.928 (log) | 0.074 | 0.892 | 0.024 | 0.898 | -0.017 (log) | 0.931 (log) |
|  | SD | -0.072 (log) | 0.974 (log) | -0.021 | 0.979 | -0.135 (log) | 0.968 (log) | -0.076 (sqrt) | 0.973 (sqrt) |
| Eigenvalue |  | 4.692 | 2.197 | 4.163 | 2.333 | 5.200 | 1.929 | 5.341 | 2.227 |
| Cumulative Proportion of Variance Explained |  | 0.521 | 0.765 | 0.462 | 0.722 | 0.578 | 0.792 | 0.593 | 0.841 |

Table 2. Factor loadings generated by Principal Components Analyses of temperature data for the three datasets for *O. humifusa* and for the RGR dataset (including all surveys) for *O. stricta.* The "T1" columns indicate the factor loadings from the first PCA axis and the "T2" columns the second PCA axis; the dataset used for the PCA is indicated in parentheses. Summary statistic abbreviations include maximum (Max.) and standard deviation (SD). Variables that were transformed prior to the PCA are indicated by the inclusion of the transformation in parentheses next to the factor loading score; transformations included the natural logarithm (log), square root (sqrt), and power function ( [^1.25] and [^0.75]). The "Rotated" row indicates which axes were rotated orthogonally to improve interpretability; PCAs of the RGR datasets were not rotated because only one axis per dataset was retained for analysis. We excluded the SD of Number of Cosecutive Days with Temperatures Below Freezing from the analysis of the RGR data because it could not be transformed to normality.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Variable | Summary Statistic | T1 (RGR) | T1 (Spring) | T2 (Spring) | T1 (Winter) | T2 (Winter) | T1 (RGR) |
| Species | Species | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. stricta |
| Maximum Temperature | Mean | -0.816 (log) | -0.045 | 0.984 | 0.101 (log) | 0.958 (log) | -0.829 |
|  | SD | 0.762 (sqrt) | 0.888 | 0.093 | 0.887 | -0.351 | 0.738 |
| Mean Degree Day | Mean | -0.9 (log) | -0.712 | 0.039 | -0.54 | 0.734 | -0.902 (sqrt) |
| Percentage of Freezing Days |  | 0.95 (sqrt) | 0.812 (sqrt) | 0.514 (sqrt) | 0.841 | 0.038 | 0.955 (sqrt) |
| Number of Cosecutive Days with Temperatures Below Freezing | Mean | 0.919 | 0.882 | 0.411 | 0.811 | 0.482 | 0.914 (^1.25) |
|  | Max. | 0.951 (sqrt) | 0.968 (sqrt) | 0.026 (sqrt) | 0.945 (log) | -0.065 (log) | 0.945 (sqrt) |
|  | SD |  | 0.942 | -0.187 | 0.866 (^0.75) | -0.172 (^0.75) |  |
| Eigenvalue |  | 4.710 | 4.685 | 1.321 | 4.164 | 1.780 | 4.687 |
| Cumulative Proportion of Variance Explained |  | 0.785 | 0.669 | 0.858 | 0.595 | 0.849 | 0.781 |
| Rotated |  | No | Yes | Yes | Yes | Yes | No |

Table 3. Correlations in the presence of the four insect species on *O. humifusa* and *O. stricta*.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Species | Insect | Native Moth | Native Scale | Invasive Moth |
| *O. stricta* | Native Bug | -0.05 | -0.065 | 0.08 |
|  | Native Moth |  | -0.014 | 0.174 |
|  | Native Scale |  |  | -0.046 |
| *O. humifusa* | Native Bug | 0.011 | 0.012 | -0.047 |
|  | Native Moth |  | 0.148 | -0.017 |
|  | Native Scale |  |  | -0.043 |

Table 3. Parameter coefficients from the best models explaining *O. humifusa* and *O. stricta* RGR and fruit presence. TO DO: Convert parameter estimates to odds ratios? How to estimate Native Moth x T?

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Vital Rate** | Fruit Presence | Fruit Presence | Fruit Presence | Fruit Presence | Fruit Presence | Fruit Presence | Fruit Presence | Relative Growth Rate | Relative Growth Rate |
| **Dataset** | Winter | Winter | Winter | Spring | Spring | Winter | Spring |  |  |
| **Species** | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. humifusa | O. stricta | O. stricta | O. humifusa | O. stricta |
| **C\_t** | 4.1 [2.77, 5.42] | 3.95 [2.72, 5.19] | 3.79 [2.57, 5.01] | 3.23 [1.622, 4.837] | 3.543 [2.016, 5.07] | 8.86 [4.89, 12.84] | 5.1717 [3.0669, 7.2765] | -0.65 [-0.87, -0.42] | -0.28 [-0.47, -0.09] |
| **Native Bug** |  |  |  | 0.876 [0.002, 1.751] |  |  |  |  |  |
| **Native Moth** | -0.34 [-1.18, 0.5] |  |  | -0.624 [-1.713, 0.464] | -0.576 [-1.601, 0.45] |  |  |  |  |
| **Native Scale** |  |  | 1.66 [0.6, 2.72] | 1.202 [-0.39, 2.794] |  |  |  |  |  |
| **Invasive Moth** |  |  |  |  |  |  |  |  | -0.42 [-0.64, -0.19] |
| **P** |  |  |  | P1 = 0.577 [-0.061, 1.215], P2 = -0.323 [-1.01, 0.363] | P1 = 0.443 [-0.124, 1.009], P2 = -0.507 [-1.023, 0.009] |  |  | P1 = -0.2 [-0.29, -0.1], P2 = 0.14 [0.06, 0.22] | P1 = -0.19 [-0.31, -0.07], P2 = 0.2 [0.09, 0.3] |
| **T** |  |  |  | T1 = 0.357 [-0.299, 1.013], T2 = 1.337 [0.26, 2.415] | T1 = 0.704 [0.249, 1.158], T2 = 0.876 [0.101, 1.651] |  |  | T1 = 0.2 [0.12, 0.28] | T1 = 0.26 [0.15, 0.37] |
| **Insect x Weather** |  |  |  |  |  |  |  |  |  |
| **P x T** |  |  |  | T1 x T2 x P1 x P2 |  |  |  |  |  |
| **Random Effect** | Plant ID, Location (Year) | Plant ID, Location (Year) | Plant ID, Location (Year) | Plant ID, Location | Plant ID, Location | Year | None | Location(Year), Plant ID | Location(Year) |
| **Upper Bound, Number of Parameters** | 4 | 2 | 4 | 16 | 8 | NA | NA | NA | NA |

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