

The role of abiotic and biotic factors in determining coexistence of multiple pollinators in the yucca–yucca moth mutualism

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The determinants of a species' geographic distribution are a combination of both abiotic and biotic factors. Environmental niche modeling of climatic factors has been instrumental in documenting the role of abiotic factors in a species' niche. Integrating this approach with data from species interactions provides a means to assess the relative roles of abiotic and biotic components. Here, we examine whether the high host specificity typically exhibited in the active pollination mutualism between yuccas and yucca moths is the result of differences in climatic niche requirements that limit yucca moth distributions or the result of competition among mutualistic moths that would co-occur on the same yucca species. We compared the species distribution models of two *Tegeticula* pollinator moths that use the geographically widespread plant *Yucca filamentosa*. *Tegeticula yuccasella* occurs throughout eastern North America whereas *T. cassandra* is restricted to the southeastern portion of the range, primarily occurring in Florida. Species distribution models demonstrate that *T. cassandra* is restricted climatically to the southeastern United States and *T. yuccasella* is predicted to be able to live across all of eastern North America. Data on moth abundances in Florida demonstrate that both moth species are present on *Y. filamentosa*; however, *T. cassandra* is numerically dominant. Taken together, the results suggest that moth geographic distributions are heavily influenced by climate, but competition among pollinating congeners will act to restrict populations of moth species that co-occur.

Determining the factors that influence a species' range in both ecological and evolutionary time has major implications for understanding contemporary patterns of species distributions as well as the structure of communities and ecosystems (following MacArthur 1972, Ricklefs and Schluter 1993, Wiens 2011, Lurgi et al. 2012). Species' range limits are primarily determined by a species' environmental niche tolerance for abiotic factors that vary in geographic space (Sexton et al. 2009). However, biotic factors such as species interactions also vary geographically and likely play pivotal roles in determining whether a species will reside in a given region (Sexton et al. 2009, Wiens 2011, Freeman and Mason 2015, Godsoe et al. 2015). For example, the absence of a host in a geographic area precludes the presence of parasitic taxa (Stewart et al. 2015), plant–pollinator interactions may be geographically limited by the availability of pollinators or plants (Moeller et al. 2012, Silva et al. 2014), and predators may need a minimum prey base to colonize and persist in a geographic region (Trainor et al. 2014, Alofs and Jackson 2015). Therefore, accurately predicting the range of a species requires using an approach that can incorporate both abiotic and biotic niche components.

One common approach to examine the geographic distribution of a taxon is species distribution modelling (SDM), a technique that uses abiotic factors associated with climate to predict the ability of a species to occupy

particular geographic areas (Phillips et al. 2006). Although this approach has performed remarkably well, one limitation is that it is currently not possible to include biotic factors into the model when analysing species distributions (Wisn et al. 2013). Species distributions predicted by SDM might, then, include geographic areas that may be unsuitable due to the presence or absence of other biota. Thus, inferences from other types of data extrinsic to SDMs may be required when evaluating the presence or absence of a focal species from a geographic area (Giannini et al. 2013).

Although combining biotic and abiotic data into SDMs remains beyond current techniques, several studies have demonstrated that it may be possible to use SDMs to infer how species interactions, particularly competition, can leave a signature on the geographic distribution of a pair of potentially competing species (Anderson et al. 2002, Gutiérrez et al. 2014, Holzmann et al. 2014, Santos et al. 2014, Freeman and Mason 2015). Competition has been demonstrated to substantially influence the geographic distribution of both closely related and ecologically similar species (Case et al. 2005, Algar et al. 2013, Pigot and Tobias 2013). Under competition, a focal species may be physiologically and ecologically adapted to the environmental conditions and biotic resources found in a given geographic area, but a superior competitor may reduce the focal species' population density or completely exclude it from the region. Anderson et al.

(2002), for instance, examined the environmental niches of two species of *Heteromys* pocket mice that occur in north-western South America. Using GARP analyses, they demonstrated that *H. australis* and *H. anomalus* could co-occur in many areas. Based on current distributions, however, *H. australis* is likely a superior competitor because it is the only species that occurs in the potential areas of sympatry. Moreover, *H. anomalus* occurs only in isolated areas that *H. australis* has not colonized historically. Gutiérrez et al. (2014) also used SDMs to infer competition between two species of mouse opossums (*Marmosa*) that occur in Panama, Colombia, and Venezuela. These two species showed similar patterns of competitive interaction. *Marmosa xerophila* appeared to be competitively dominant in contact zones and *M. robinsoni* occurred only in geographically isolated areas on peninsulas, even though both species had similar environmental niche requirements.

As highlighted in the above two studies, competition is most likely to be important in dictating geographic distributions when species have a high degree of resource use overlap and share similar morphologies and habitat use requirements (MacArthur and Levins 1967, HilleRisLambers et al. 2012). In particular, closely related species are more likely to have similar ecological requirements and thus experience heightened competition if they remain in the same geographic area but do not evolve differences in resource use (Burns and Strauss 2011, Violle et al. 2011, Rabosky 2013). Radiations of organisms colonizing island archipelagos, for example, demonstrate how competition can fuel changes in resource use and speciation within a lineage to reduce resource overlap (Grant and Grant 2006, Foster et al. 2008, Losos 2009, Parent and Crespi 2009). Consequently, competition may be one of the major factors in addition to the abiotic niche that determines the geographic distributions of closely-related species.

Competition among closely related species may be particularly important in determining the geographic distributions of taxa involved in obligate pollinating–seed feeding mutualisms such as those between yuccas and yucca moths, figs and fig wasps, leaf-flower trees and leaf-flower moths. A key feature of these mutualisms is that the pollinators tend to be highly specialised to their host plants (Pellmyr and Leebens-Mack 2000, Kato et al. 2003, Cruaud et al. 2012). The insect taxa pollinate flowers either actively or passively and then deposit eggs into the flower (Pellmyr 1997). The larvae consume a portion of the seeds to complete development. The overall interaction is relatively simple in that plants provide their respective pollinating insect with larval food substrate (seeds) in protected fruit tissue that is accessible only to specialised insect species. Thus, multiple species of pollinating–seed feeders on the same plants would compete for key limiting resources – access to oviposition sites and seeds. As such, a characteristic of these interactions is that there is usually only one pollinator species per host plant species and, in instances where there are multiple pollinator species per host plant species, the pollinator species are generally replaced across the geographic range of the host plant or there is a strong difference in the relative densities of the species (Althoff et al. 2012, Hembry et al. 2013, Darwell et al. 2014).

For the pollinating–seed feeding mutualism between yuccas and yucca moths, specialisation by pollinators is the norm (Davis 1967, Powell 1992). Almost all of the 30 plus species of *Yucca* are pollinated by a highly host-specific pollinator moth species in the genus *Tegeticula*. One of the potential contributing factors to this pattern of high host specificity in this interaction might be competition between pollinator moths. This competition is mediated by the plant because yuccas can use selective abscission to regulate moth egg loads within flowers (Pellmyr and Huth 1994). When a female moth deposits eggs next to the developing yucca ovules, the ovipositor incidentally causes ovule damage. Marr and Pellmyr (2003) demonstrated that mechanically increasing ovule damage with a simulated ovipositor increases the probability that a flower will be abscised from the plant. Flowers with many oviposition attempts (i.e. potentially more eggs) are preferentially abscised. Thus, co-occurring pollinator species that deposit eggs next to plant ovules, would not only compete for access to oviposition sites, but also have to contend with increased egg/larval mortality as a consequence of the plant's response to damage.

Competition between pollinator species that lay eggs next to plant ovules may also have spurred the evolution of moth species that avoid the mechanism of selective abscission. This is evidenced by the evolution of pollinator species that differ in oviposition strategy (Addicott and Bao 1999, Pellmyr 1999, Pellmyr and Leebens-Mack 2000, Althoff et al. 2006). For instance, three pollinator species deposit eggs just within or below the pistil surface and do not damage plant ovules such that selective abscission is not triggered (Pellmyr 1999). This shift in oviposition strategy might allow coexistence of multiple pollinator species on the same yucca species at a given locality, yet there are few regions in which multiple pollinator species coexist on the same plants (Addicott and Bao 1999, Csotonyi and Addicott 2001). There has also been the evolution of at least two cheater species. These species have lost the ability to pollinate and wait until the period of selective abscission has passed before depositing eggs into developing fruit, either early or late in fruit development (Pellmyr et al. 1996, Pellmyr 1999). The cheater species have broad geographic ranges in which they co-occur with pollinator species (Pellmyr 1999). Geographic replacement of pollinator species suggest that pollinators, irrespective of oviposition strategy, may compete with one another for access to oviposition sites (i.e. flowers) or seeds.

One of the signatures of competition would be the geographic exclusion of pollinator species from different yucca species by a resident pollinator. Evaluating this is somewhat complicated in the sense that *Yucca* species generally have allopatric distributions, making it difficult to determine if the non-overlapping geographic ranges of pollinator species are primarily determined by other factors such as local adaptation to *Yucca* species, historical biogeography, or dispersal limitation. The one exception is in the southeastern United States where there is overlap between two pollinator species on *Yucca filamentosa*. The widespread *Tegeticula yuccasella*, appears to be a generalist that pollinates and feeds on seven *Yucca* species across its geographic range that stretches across the easternmost two-thirds of North America (Fig. 1) (Pellmyr 1999). In Florida and southern

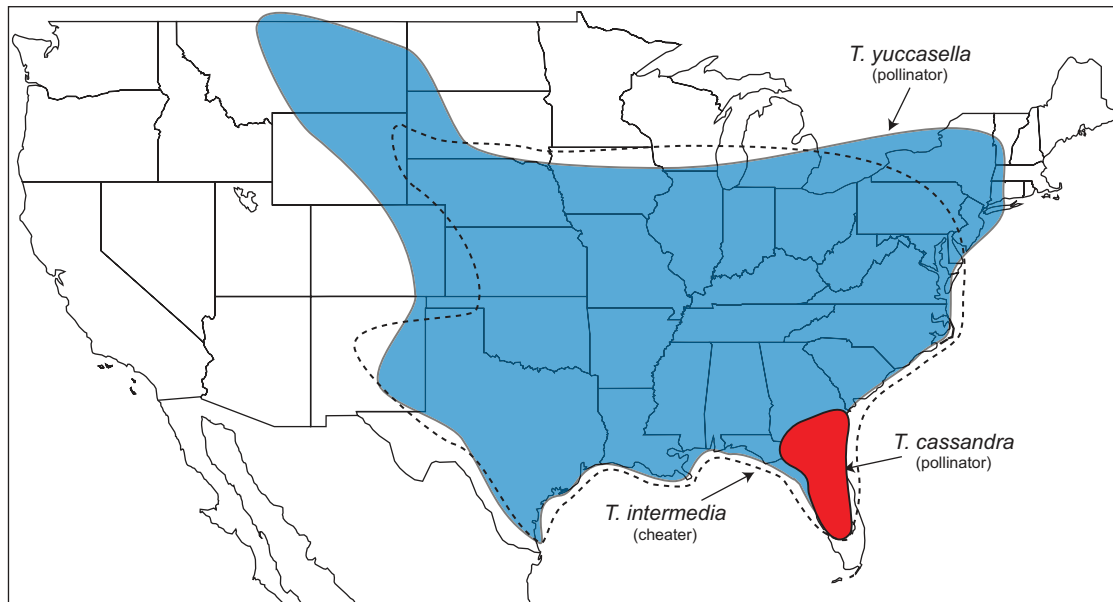


Figure 1. Geographic distributions of the two pollinator yucca moths, *Tegeticula yuccasella* and *T. cassandra*, and the cheater moth *T. intermedia*.

Georgia, *T. yuccasella* comes into contact with a second pollinator, *T. cassandra*, that also uses *Y. filamentosa*. Unlike *T. yuccasella*, *T. cassandra* is geographically restricted to this region (Segraves and Pellmyr 2004) (Fig. 1). Interestingly, the cheater *T. intermedia* which is the sister species to *T. cassandra*, occurs across eastern North America and coexists with both pollinator species, although at lower densities (Marr et al. 2001). Ecologically, the only difference between *T. cassandra* and *T. intermedia* is that the former is a pollinator and deposits eggs into flowers while the latter cannot pollinate and places its eggs into young fruit.

The fact that the cheater moth *T. intermedia* has a much expanded range in contrast to its sister species *T. cassandra* suggests that there may be competition between the pollinator species that has influenced their geographic distributions. Differences in oviposition modes between pollinator yucca moths has been suggested to influence the ability of moths to invade or persist in populations where there is a resident pollinator already established (Csotonyi and Addicott 2001). Both *T. yuccasella* and *T. cassandra* use *Y. filamentosa* flowers as oviposition sites but differ in how they place their eggs. While *T. yuccasella* displays the more typical *Tegeticula* oviposition mode of using a long, thin ovipositor to deposit eggs next to yucca seeds within the fruit locules (locule-oviposition), *T. cassandra* deposits eggs just below the plant surface (superficial-oviposition) at the top of the flower with a short, broad ovipositor (Pellmyr 1999, Segraves 2003). Thus, the question remains whether competition between these pollinators drives their geographic distributions.

Here, we investigate signatures of competitive exclusion by examining niche overlap in both geographic and environmental niche space between the pollinators, *T. yuccasella* and *T. cassandra*. We construct SDMs for both species to identify regions of potential sympatry. We also analyse climatic environmental data to investigate the niche tolerances of each species to determine whether their occupied niche profiles suggest if they could likely exist in each other's geographic range or are currently limited by the ability to

tolerate differences in local environments. Finally, we incorporate data on the abundance of each pollinator species at a key locality to further assess if competition among pollinator species is a major factor influencing the distributions of *T. yuccasella* and *T. cassandra* in southeastern North America.

Methods

Data sources

We compiled geographic locations of *T. yuccasella* and *T. cassandra* from across North America from the primary literature (Davis 1967, Pellmyr 1999, Leebens-Mack and Pellmyr 2004, Segraves and Pellmyr 2004, Althoff et al. 2006, 2012) as well as field collections performed by the authors over the last two decades (Fig. 1 and Supplementary material Appendix 1, Table A1). Adults and larvae collected from each species were identified using a combination of morphological and molecular analyses. From the compiled locations, we spatially filtered locality data for each species to include the maximum number of locations that were at least 10 km apart (Anderson and Raza 2010, Boria et al. 2014). This was done to reduce biases in the sampling scheme that could result in increased sampling in more easily accessible regions. The final, filtered datasets contained 160 unique localities for *T. yuccasella* and 22 for *T. cassandra*. The small number of localities for *T. cassandra* is not for lack of sampling, but is the result of the smaller geographic range of this species. This sample size is sufficient for evaluating SDMs (Pearson et al. 2007). For the environmental data, we used the 19 WorldClim bioclimatic variables at 30" resolution (= 0.86 km² pixels) (Hijmans et al. 2005, <<http://biogeo.berkeley.edu/worldclim/worldclim.htm>>). The 19 WorldClim variables are derived from combinations of temperature, precipitation and seasonality records and have become the standard dataset for baseline predictions of the geographic distributions of species.

Species distribution models

We employed Maxent ver. 3.3.3k which uses the maximum entropy algorithm to construct SDMs (Phillips et al. 2006, Phillips and Dudik 2008). In order to fit the correct model and avoid model overfitting, we used the 'ENMeval' package (Muscarella et al. 2014) in R (R Development Core Team) to determine the optimal feature class (FC) and regularisation multiplier (RM) settings. Model evaluation was conducted for each species using only environmental data from the species' range. We used the R package adehabitatHR (Calenge 2006) to create a mask as a dummy variable delimited by the 'minimum convex polygon' around all species' locations and a 0.5° buffer zone. To partition occurrence localities into testing and training bins (folds) for *k*-fold cross-validation, we used the 'checkerboard1' (Muscarella et al. 2014) method for *T. yuccasella* and the 'jackknife' method for *T. cassandra*, which is appropriate for small numbers of occurrence records (Pearson et al. 2007). FC and RM settings were obtained by choosing the settings that returned a $\Delta AICc$ score of zero (Muscarella et al. 2014).

For each species, 15 SDMs across the entire study region were run in Maxent with the chosen FC and RM settings and a 10% training threshold rule which rejects the lowest 10% of predicted values (Pearson et al. 2007). This allowed us to transform probabilistic SDMs into binary predictions of suitable vs non-suitable climatic conditions at each pixel. To then construct a single 'average' binary SDM from the 15 constructed binary models, custom Python scripts (available from the authors) were built to merge SDMs using simple majority-rule to determine if a pixel should be considered suitable for the presence of the study species. Finally, Python scripts were again employed to merge the final SDMs for each species into a single composite SDM that indicates for each pixel: predicted absence, predicted presence of the first species only, predicted presence of the second species only, and predicted presence of both species (i.e. potential sympatry).

Niche evaluation

We used the methods developed by Broennimann et al. (2012) in the R package 'ecospat' to assess whether *T. yuccasella* and *T. cassandra* have similar climatic niche requirements and to confirm our SDM predictions that the two species could occupy similar ranges. First, we generated 1000 and 500 random GPS points (R package 'maptools'; <<http://r-forge.r-project.org/projects/maptools/>>) across the ranges of *T. yuccasella* and *T. cassandra*, respectively, and extracted the 19 WorldClim variables from these points. This provided a 'background' dataset of environmental values. In the same manner, 19 WorldClim were extracted from the actual locations of *T. yuccasella* and *T. cassandra*. The 'ecospat' software then uses an ordination approach to calculate the occurrence density and climatic factor density along the first two principal component axes of the environmental data. These are then used to evaluate measures of niche overlap along these axes. The software then builds on the methods of Warren et al. (2008) using Schoener's D statistic (Schoener 1970) to evaluate niche equivalency and niche similarity. D values

range from 0 indicating no overlap to 1 indicating complete overlap. For niche equivalency, the occurrence data are pooled and randomly split into two datasets and the D statistic is calculated. This is repeated 100 times and the distribution of D values is compared against the actual D for the two SDMs for the species. The niche similarity test determines if the D statistic for two species is significantly different from a distribution of D values generated from the actual occurrence data of one species versus 100 simulated datasets (i.e. from environmental data for random locations derived from the background data). The test is then reversed for the second species. Analyses were conducted across the entire current range of both species and then again for data collected just in the southeastern United States. The southeastern United States is the native range of *Y. filamentosa* and populations further north and west are considered to be the result of anthropogenic activity largely through their use as horticultural plants (Althoff and Pellmyr 2002). Thus, the expanded range of *T. yuccasella* is likely an artefact of colonization or anthropogenic transport to new localities that has allowed it to colonize all populations of *Y. filamentosa* outside of the plant's ancestral range. We were concerned that this fact may inflate the estimates of niche differentiation among the moth species because it does not represent the historical ranges in which the two species interacted.

Occurrence of moth species in sympatry

In addition to SDMs, insect surveys (2001–2003, 2010) near the Archbold Biological Station in Lake Placid, Florida (27°15'22"N, 81°22'57"W) were used to examine the relative numbers of the pollinators *T. yuccasella* and *T. cassandra* in a large and stable population of *Y. filamentosa*. This site has been used extensively in previous research on the ecological dynamics of the mutualism between *T. cassandra* and *Y. filamentosa* (Segraves 2003, Althoff et al. 2005, 2013, Segraves et al. 2005, 2008). Briefly, all flowering *Y. filamentosa* within a 500 ha area were visited daily and all the insect visitors on and within the inflorescences were identified and counted. Surveys covered the entire flowering period from early May to late June. We also examined the relative abundances of each species from larval rearings at this site. In 2002, fifth instar larvae were collected from fruits from plants throughout the survey site, allowed to overwinter in containers placed in the soil, and checked the following year for adult emergence (Segraves et al. 2008).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.m6k5k>> (Darwell et al. 2016).

Results

Species distribution models and areas of potential sympatry

Species distribution models (SDMs) constructed in Maxent indicated abiotically suitable areas largely congruent with the known geographic distributions for both species in North America (Fig. 2). There are, however, abiotically

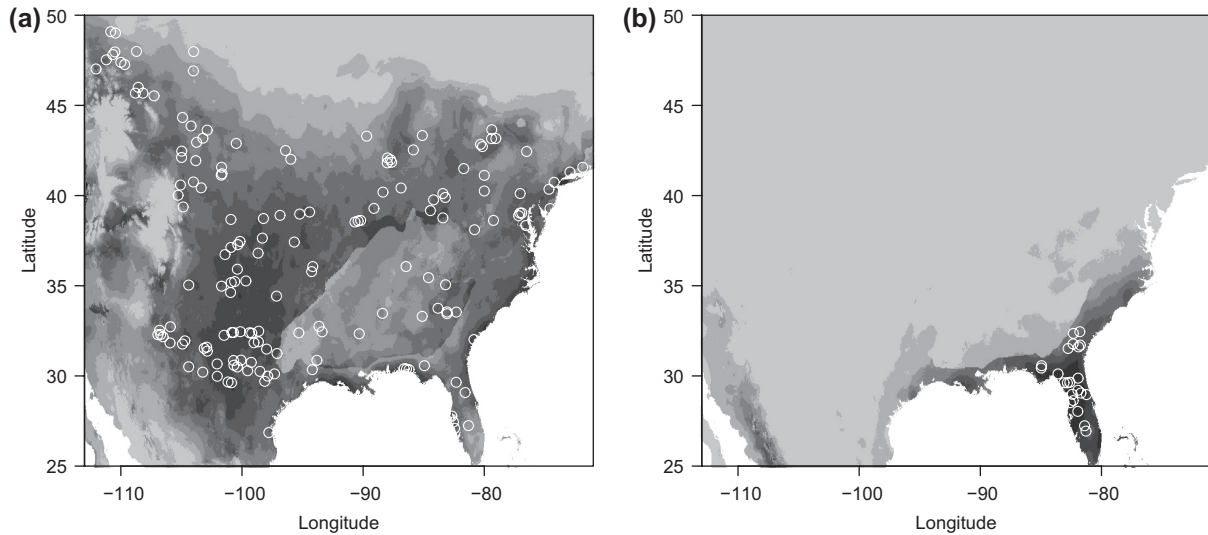


Figure 2. Models of abiotically suitable areas based on species distribution modelling for the pollinator yucca moths (a) *Tegeticula yuccasella* and (b) *T. cassandra*. Darker regions indicate more suitable climatic conditions. Circles denote localities that were at least 10 km apart.

suitable areas for both species outside of the currently known ranges. For *T. cassandra*, areas along coastal margins both westward and northward from Florida appear to be suitable habitats. For *T. yuccasella*, the SDM suggests northern and central Florida as suitable areas. When overlapped, the models predicted areas of potential sympatry across most of Florida (except for the southern regions of Florida where *T. yuccasella* is not favoured) and coastal Georgia (Fig. 3). Two disjunct areas of potential sympatry also occurred around coastal areas of eastern Louisiana and southern North Carolina where neither species has been recorded because the host plant *Y. filamentosa* does not occur there. No other regions within North America were predicted as areas of potential sympatry.

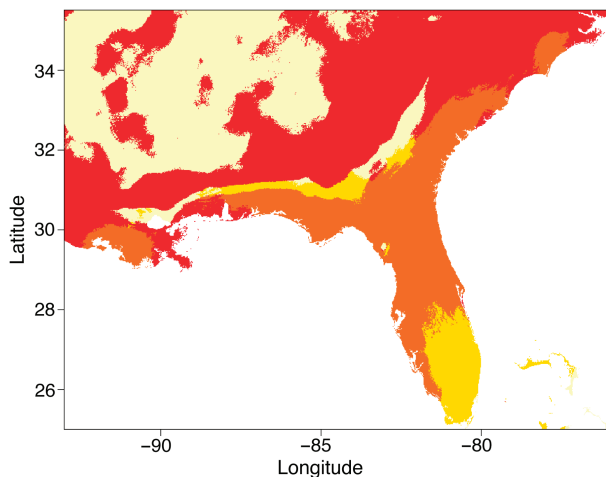


Figure 3. Overlapped species distribution models of *Tegeticula yuccasella* and *T. cassandra* indicating potential areas of sympatry in the south-eastern United States. Red indicates regions suitable for *T. yuccasella* only; yellow indicates regions suitable for *T. cassandra* only; orange indicates regions predicted for both species co-existence. Two disjunct areas of potential sympatry are predicted in eastern Louisiana and southern North Carolina.

Statistical evaluation of niche characteristics

Niche equivalency and niche similarity tests based on the WorldClim climatic data from across the entire combined ranges of both moth species suggested that *T. yuccasella* and *T. cassandra* occupy distinct niches (Table 1). The niche equivalency test resulted in a Schoener's D value significantly less than the mean value from 100 replicates of randomly reassigning climatic data between groups. This result suggests that the niches of the two species are not identical. The niche similarity tests could not reject the null hypothesis of niche dissimilarity. Taken together, the results suggest that there is differentiation in the niches, as defined by the WorldClim data, when drawing samples from across the entire range of both moth species. In contrast, tests using a more focused climatic dataset from the historical ranges of both species in the southeastern United States demonstrated that the niche characteristics of the two moth species are not different. Both the niche equivalency and similarity tests demonstrated that the two niches were more similar than expected by chance.

Principal component analyses on climatic data from across the entire combined ranges of both species suggest that *T. yuccasella* and *T. cassandra* occupy distinct zones of the first two principal climatic niche axes (Fig. 4a, b). *T. yuccasella* occupies three clearly distinguishable zones, suggesting that populations of this species occur in different regions of climatic niche space, whereas *T. cassandra* occupies a single region. Focused principal component analyses on climatic data from localities only in southeastern North America also suggest that *T. yuccasella* and *T. cassandra* occupy distinct zones of climatic niche space, but there are a range of climatic conditions that both species could occupy (Fig. 4c, d). This is consistent with the results from the niche equivalency and niche similarity tests.

Surveys of adult moths on *Y. filamentosa* near the Archbold Biological Station demonstrated that *T. cassandra* was the numerically dominant species at this site. Insect surveys from four flowering seasons (2001–2003, and 2010) detected 1816 *T. cassandra* in contrast to 28 *T. yuccasella*.

Table 1. Results of niche equivalency and niche similarity tests for *T. yuccasella* and *T. cassandra*. Column labels are obs. – observed value of Schoener’s D between actual SDMs of each species; μ – mean value of Schoener’s D generated from 100 simulated datasets; p – p-value; meaning – interpretation of test results.

Niche test	Entire combined ranges				Southeastern United States			
	obs.	μ	p	meaning	obs.	μ	p	meaning
Equivalency	0.116	0.847	<0.02	Different niches	0.521	0.746	0.059	Equivalent niches
Similarity 1	0.116	0.084	0.119	Different niches	0.521	0.266	<0.001	Similar niches
Similarity 2	0.116	0.072	0.178	Different niches	0.521	0.333	<0.010	Similar niches

Larval rearings in 2002 yielded 161 *T. cassandra* and 5 *T. yuccasella*. This locality is at the southern extent of *T. cassandra*, suggesting that it is possible for *T. yuccasella* to occur throughout the entire range of *T. cassandra*.

Discussion

Determining the factors that govern the contemporary distributions of species can help us understand the evolutionary and ecological processes that have shaped the macroecological patterns of biodiversity on Earth. Typically, the primary consideration when investigating determinants of a species range is the abiotic tolerances that determine occupancy in environmentally suitable areas (Sexton et al.

2009). The success of species distribution modelling in accurately predicting species ranges and occupancy rates across many types of organisms clearly demonstrates the importance of abiotic factors (Peterson 2003). In some instances, however, species may be absent or significantly underrepresented in a geographic region that appears to have suitable abiotic conditions and no obvious geographic barriers to colonisation (Anderson et al. 2002, Gutiérrez et al. 2014). In such cases, biotically mediated factors such as the presence or absence of additional ecologically important species are likely governing its distribution. For example, if the identified region harbours a closely-related, ecologically similar species, then the most parsimonious explanation is that the occupying species is competitively excluding the absent species.

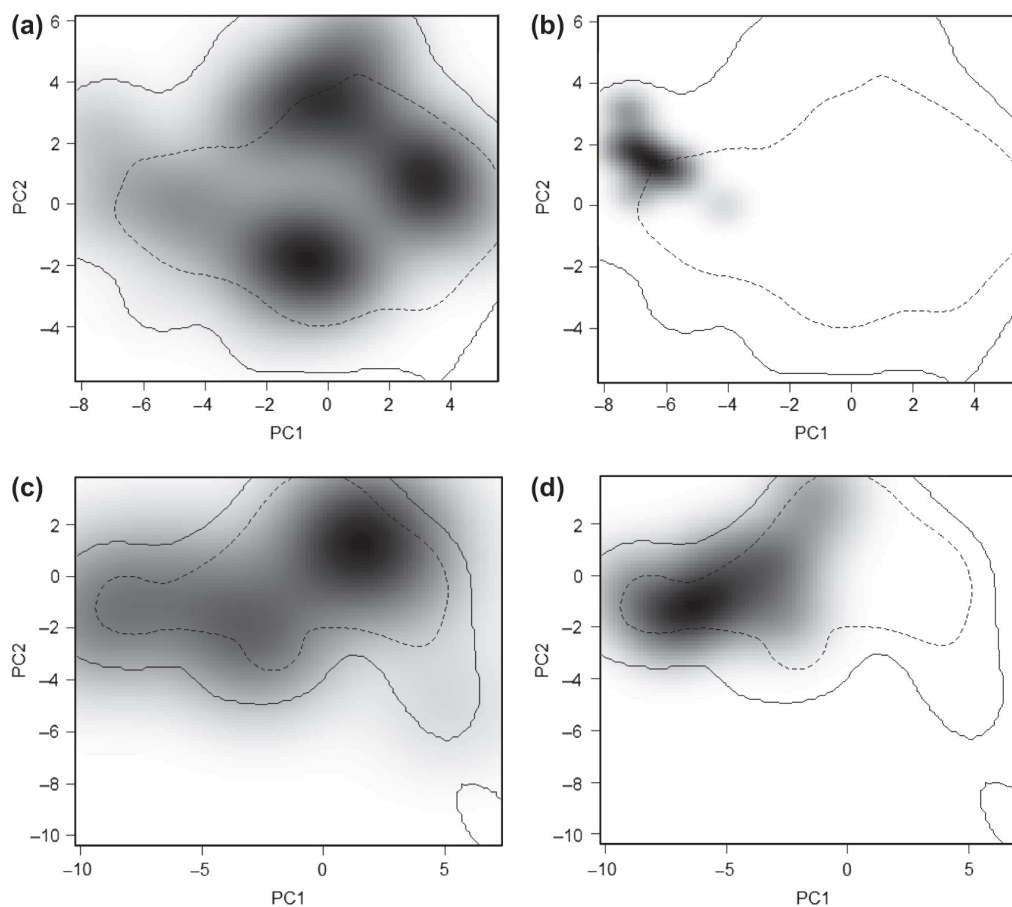


Figure 4. Niche occupancy of *T. yuccasella* (left panels) and *T. cassandra* (right panels) based on the first two axes of principal component space derived from climatic data from the entire combined ranges of *T. yuccasella* and *T. cassandra* (a and b), and from climatic data from just localities occurring in southeastern North America (c and d). Darker areas represent greater occupancy. Solid contour line is 100% of suitable niche space and dashed line is 50% of niche space.

For the obligate pollination mutualism between *Tegeticula* moth and *Yucca* plant species, closely-related pollinator moths and host plant species generally have allopatric distributions that correspond with known biogeographic regions of North America (Pellmyr 1999, Pellmyr et al. 2007, Althoff et al. 2012). In general, the pollinating moths are extremely host-specific and typically there is a single pollinator species for a *Yucca* species. The high host specificity of the moths could be a result of competition among pollinator species that would otherwise co-occur on the same host plant species, a result of the mutualistic interaction between pollinator and plant, biogeographic history, or some combination of all three. Althoff et al. (2012) suggest that based on current range distributions and co-speciation analyses between moths and yuccas, that geographic isolation might be the best explanation for the high host specificity observed rather than selection caused by the mutualism or interactions with other moth species.

There are, however, a few instances in which pollinator species share a host *Yucca* species, either in sympatry, or replace one another over the geographic range of the plant (Addicott and Bao 1999, Csotonyi and Addicott 2001, Segraves and Pellmyr 2004). These situations allow tests of potential competition among pollinator species that may contribute to host specificity and moth species' ranges. Across most of eastern North America, there is only one *Yucca* species, *Y. filamentosa*, that has a geographic range that extends from southern Canada to Florida and Texas. The pollinator, *T. yuccasella* is the sole pollinator of *Y. filamentosa*, except in southeastern Georgia and most of Florida. In these localities, *T. cassandra* is the only pollinator species or is numerically dominant. The replacement of *T. yuccasella* by *T. cassandra* suggests that there may be biotic factors that exclude *T. yuccasella* from *Y. filamentosa*, given that abiotic factors are not restricting *T. yuccasella* from living in southeastern Georgia and Florida. Natural enemies are unlikely to explain this pattern given that there are no parasitoids that attack either moth species in the southeastern United States nor are there differences in the natural enemy community in Florida as compared to other localities. Hundreds of hours of moth observations and thousands of fruit dissections for larval retrieval suggest an attack rate of less than one percent for both species (Althoff unpubl.).

The niche modelling and niche evaluation analyses of abiotic factors, suggest that there is no reason why *T. yuccasella* should be virtually excluded from *Y. filamentosa* in southeastern Georgia and Florida. The combined SDMs predict that both moth species should be able to tolerate conditions across this region (Fig. 3). Although niche evaluation analyses using climatic data from the entire range of both species suggest that the two moth species have statistically divergent niche requirements, a more focused analysis restricted to climatic data from the native range of *Y. filamentosa* in the southeastern United States suggests niche overlap (Table 1). The disparity between the two niche evaluation analyses is better understood by a detailed consideration of niche occupancy in the first two principal component axes of climatic data across the entire range of both species. For *T. yuccasella*, there are three distinct areas of niche occupancy indicating niche space occupied by different subsets of populations (Fig. 4a). *Tegeticula cassandra* occupies a niche space that

is distinct from these regions (Fig. 4b). The analysis conducted on climatic data for localities from the native range of *Y. filamentosa* in the southeastern United States, however, demonstrates that *T. cassandra* and *T. yuccasella* overlap in niche space (Fig. 4c, d). Therefore, because of its much larger geographic range, *T. yuccasella* has a much broader niche than *T. cassandra*, but there is a range of niche space in which both species are predicted to be able to live.

Together, the results suggest a pattern of competition between the pollinator species as has been implicated in two previous studies of competition employing SDMs (Anderson et al. 2002, Gutiérrez et al. 2014); yet, for the yucca moths there are several key differences that present a particularly compelling argument. Previous SDMs on pocket mice and mouse opossums show parapatric species distributions where only one species occurs in potential areas of sympatry. A parapatric pattern, however, may also be caused by some additional unrecognised factor(s) that influence distribution patterns. For example, immigration may be restricted by some unknown biogeographic barrier for the absent species or there may be some unknown critical habitat or dietary requirement lacking from the region. In contrast, for *Tegeticula* pollinators, the insect survey data from *Y. filamentosa* near the Archbold Biological Station in south-central Florida demonstrates that *T. yuccasella* can occur throughout the range of *T. cassandra*. Both adult moths and larvae were present at this site at the southern edge of *T. cassandra*'s range; thus, there is not complete exclusion of *T. yuccasella* from the range of *T. cassandra*. Instead, the survey data demonstrate that over a period of ten years, *T. yuccasella* is present at extremely low abundances; that is, only one in every 60 moths is *T. yuccasella*. Because both moth species rely on the same resource (i.e. yucca flowers and seeds), competition appears to be playing a role in the virtual exclusion of *T. yuccasella* throughout the range of *T. cassandra*.

Competition between *T. yuccasella* and *T. cassandra* may occur in two ways. First, competition for oviposition sites could be driven by how the moth species deposit eggs into flowers. The locule-ovipositing *T. yuccasella* deposits eggs next to yucca ovules and females inadvertently damage ovules during oviposition. This damage is used as a mechanism by the host plant to selectively abscise flowers that have a large number of damaged ovules, and by doing so, the plants kill the moth eggs and larvae within abscised flowers (Pellmyr and Huth 1994, Marr and Pellmyr 2003). *Tegeticula yuccasella* is at a disadvantage in terms of the number of larvae that can feed within fruit as compared to *T. cassandra* that deposits eggs just below the pistil surface and does not trigger selective abscission. Thus, *T. yuccasella* suffers additional selective mortality which may make it difficult for it to reach high densities in the presence of *T. cassandra*. Second, competition could also occur via the seed resource. Although yucca seeds do not appear to be a limiting resource (Marr et al. 2001), larvae may exploitatively interfere with one another through larval predation. The larvae of *T. yuccasella* are smaller than *T. cassandra*, making them subject to predation by *T. cassandra*. During feeding, moth larvae will consume one another as they chew through the rows of seeds with the larger larva consuming smaller ones (Segraves unpubl.). Thus, *T. yuccasella* has to contend with both additional mortality due to selective

abscission and larval cannibalism when co-occurring with *T. cassandra*.

Testing these ideas in other yucca moth species are limited by allopatric distributions; however, there is at least one known contact zone in which another locule- and superficial-ovipositing pollinator species appear to co-occur at similar densities. On the Kanab Plateau in Utah, there are several geographically close populations of *Y. kanabensis* in which *T. altiplanella*, a locule-ovipositing pollinator, exists with *T. superficiella*, a superficial-ovipositing pollinator species. Csotonyi and Addicott (2001) demonstrate that *T. altiplanella* maintained similar densities over a 12-yr period. They suggested that fluctuations in population densities of the two species might lead to stable coexistence in the Kanab Plateau region. When moth densities of both species are low, flowers with locule-ovipositions by *T. altiplanella* would often be retained because many flowers on a plant would not be pollinated. When moth population densities are high, locule species are often retained irrespective of levels of abscission because all flowers have some level of ovule damage due to oviposition and there are very few flowers that only have *T. superficiella* ovipositions. Only at intermediate moth densities would *T. superficiella* be able to outcompete *T. altiplanella*. At this density, there would be many flowers that were used by *T. superficiella* only, and the flowers used by *T. altiplanella* would be preferentially abscised due to ovule damage.

In Florida, where the balance between the *T. yuccasella* and *T. cassandra* densities is strongly skewed towards *T. cassandra*, it may very difficult for *T. yuccasella* to reach parity like *T. altiplanella* in Utah. At the current moth densities, plants would preferentially retain flowers that were not damaged, thus putting *T. yuccasella* at a disadvantage relative to *T. cassandra*. Additional evidence that *T. yuccasella* and *T. cassandra* are competing for access to flowers comes from geographic distribution data for the cheater moth *T. intermedia*. This moth species has lost the ability to pollinate flowers and deposits its eggs into young fruit of yuccas, after the period of selective floral abscission (Pellmyr 1999, Segraves et al. 2008). *Tegeticula intermedia* is also the sister taxon to *T. cassandra* and deposits its eggs superficially (Althoff et al. 2006). Unlike *T. cassandra*, however, *T. intermedia* has expanded its range to all of eastern North America and Florida, co-occurring with *T. yuccasella*. This geographic distribution is expected given that access to flowers is no longer important to *T. intermedia*, thus releasing it from competition for oviposition sites. A similar pattern exists with another cheater species, *T. corruptrix* in western North America (Pellmyr 1999). This species deposits eggs into mature fruit and co-occurs with different pollinator species across its broad geographic range. In contrast, most pollinator species have more restricted ranges and do not co-occur on the same *Yucca* species at a locality (Pellmyr 1999, Althoff et al. 2012). Moreover, the distribution of *T. intermedia* also suggests that *T. cassandra* is unlikely to be dispersal limited because the moths are ecologically similar and of the same size (Pellmyr 1999). The niche analyses suggest that there are abiotic factors that limit *T. cassandra*'s distribution to Florida and Georgia where it appears to be a stronger competitor that outcompetes *T. yuccasella*.

In conclusion, there appears no obvious reason why *T. yuccasella* should be unable to successfully colonise and flourish on *Y. filamentosa* in Florida as it does in other parts of its range. In particular, the co-occurrence of two functionally similar pollinator moth species with the same differentiation in oviposition strategies on *Y. kanabensis* in Utah further supports this proposal. Despite the potential for other influencing factors, there is strong evidence that *T. cassandra* appears to be preventing *T. yuccasella* from fully using *Y. filamentosa* in Florida. Selective abscission of flowers due to ovule damage during oviposition would result in enhanced mortality for *T. yuccasella*, whereas flowers pollinated by and containing larvae of *T. cassandra* would be more likely to be retained. The presence of *T. yuccasella* at extremely low densities in Florida corroborates both the results from species distribution modelling based on climatic factors and the hypothesis that *T. cassandra* is a better competitor in Florida.

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Supplementary material (Appendix ECOG-02193 at <www.ecography.org/appendix/ecog-02193>). Appendix 1.