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There goes the neighborhood: apparent competition between invasive and native orchids mediated by a specialist florivorous weevil

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Abstract The exotic orchid, *Spathoglottis plicata*, has naturalized and spread rapidly over Puerto Rico where it is generally considered to be innocuous. It is abundant and occupies the same habitat as the native orchid, *Bletia patula*. The two are hosts to the same native weevil, *Stethobaris polita*, a specialist on orchid flowers. We ask whether the weevils mediate apparent competition between the two orchids. We monitored weevil populations, floral damage and fruit set in *B. patula* in the presence and absence of *S. plicata*. We also experimentally tested whether weevils preferred one species over the other. Finally, we modeled the distribution of both orchid species to predict the extent by which the two species may interact in Puerto Rico. We found a significantly lower number of weevils and a higher fruit set for *B. patula* where *S. plicata* is absent, indicative that apparent competition is occurring. The choice experiments show that weevils prefer flowers of *S. plicata* over those of *B. patula*, but *B. patula* still sustained considerable damage. The current distribution of the native *B. patula* is nearly limited to the northern karst region of Puerto Rico. The naturalized *S. plicata* has a broader range and the models predict that its distribution will strongly overlap with that of *B. patula*. We expect the *S. plicata* invasion to continue and affect native orchids through apparent competition as long as the presence of *S. plicata* maintains elevated weevil populations. Thus, even seemingly harmless invasive orchids can have subtle but significant negative consequences.

Introduction

Invasive species, organisms that establish viable populations in a zone outside their native range (Richardson et al. 2000; Lockwood et al. 2007; Simberloff 2009), can have both direct and indirect effects on biotic interactions and abiotic conditions (Gordon 1998; Simberloff and Von Hollen 1999; Ricciardi 2001; Russell and Louda 2005; White et al. 2006; Orrock et al. 2008). Indirect effects are how one species alters the effect that another species has on a third (Strauss 1991). Such effects are not as well known as direct effects because they can be both subtle and complex. The most commonly described indirect effect is apparent competition, which is often conveyed when a prey species becomes more abundant resulting in an increase in predator densities. This

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augments predation on a second species, negatively affecting its population growth (Holt 1977; Schmitt 1987; Rand 2003; White et al. 2006; Orrock et al. 2008). Thus, apparent competition involves two or more species with at least one being negatively affected because they share a common herbivore, pathogen, predator, or prey (Hoogendoorn and Heimpel 2002; Rand 2003; Noonburg and Byers 2005; White et al. 2006).

The spread of invasive species in their new ranges is sometimes possible because their natural enemies have been left behind (enemy release hypothesis; Keane and Crawley 2002). Other invaders encounter novel enemies, thus opening the possibility of associational susceptibility or defense within the community (Russell and Louda 2005; Barbosa et al. 2009). In fact, apparent competition can be a common side effect when an invasive species becomes integrated into a plant community. Documented cases of apparent competition have been found in invasive prey–invasive predator–native prey scenarios (Rand and Louda 2004; Lau and Strauss 2005; Russell et al. 2007), and less commonly in systems where the herbivore is a native species with broad diet preferences (Orrock et al. 2008). The magnitude of apparent competition may be affected by a number of factors including prey or host preferences and spillover effects as classical biological control cases have revealed (Schmitt 1987; Holt and Hochberg 2001; Noonburg and Byers 2005; Sheppard et al. 2005). The result is a bridge linking invasive with native species by interactions of a third party.

Puerto Rico, like other islands, has become host to numerous invasive species (Daehler 2006; Kueffer et al. 2010). A few alien orchids are among those that are rapidly colonizing habitats across the island, although they are generally considered innocuous (Ackerman 2007). One of these orchids is *Spathoglottis plicata* Bl., an Asiatic species, which has now invaded the same habitats as the native orchid, *Bletia patula* Graham. The two sympatric orchids share a native florivorous weevil, *Stethobaris polita* Chevrolat, an orchid specialist. Adults consume perianth parts, lay eggs in fruits, and the larvae consume developing seeds. While the consequences of seed predation are obvious, that of florivores may be more subtle, indirect and mediated by pollinator behavior (Strauss et al. 2004; Leavitt and Robertson 2006; McCall and Irwin 2006; Barbosa et al. 2009). For

example, the lip of an orchid is often particularly important to attract and orient pollinators, provide a landing platform, and position them to deposit pollen on the stigma and remove the pollinarium as they depart (Darwin 1877; van der Pijl and Dodson 1966; Dressler 1981). Any changes through florivory may fracture the integrated functions (Malo et al. 2001; McCall 2008). The potential for a tripartite interaction involving apparent competition exists, although it would be unusual for indirect interactions between native and exotic species driven by a native specialist.

We sought to determine whether *Spathoglottis plicata* is having indirect effects on the reproductive success of *Bletia patula* by elevating the occurrence of the weevil, increasing the extent of floral damage and reducing the frequencies of pollinator visits. As weevil frequencies may be a consequence of preferences and possibly spillover, we experimentally tested in vitro whether one orchid species is more palatable or preferable than the other. Finally we predict the possible distribution of both orchids, calculate the area of sympatry where the interaction likely occurs, and assess whether it will likely change in the future. The severity of apparent competition and the geographical extent of the interaction may reveal the level of urgency for the development of management practices that promote the stability of the native community (Wiggins et al. 2010; Trethowan et al. 2011).

Materials and methods

Plant descriptions

Bletia patula is a terrestrial orchid, known from southern Florida, Cuba, Hispaniola and Puerto Rico (Ackerman 2012a). Populations mostly occur at low elevations in limestone regions and exposed cliffs, often along roadsides. The flowers are large, showy and nectarless. Pollination is via food deception, and fruit set is low (11–28 %) relative to rewarding species (Ackerman 1995; Ackerman and Carromero 2005; Tremblay et al. 2005). Reproductive success in such orchids is regarded to be pollination- and seed-limited (Calvo and Horvitz 1990; Ackerman et al. 1996). In Puerto Rico, most plants have magenta flowers; lavender and white color forms are quite rare and were not part of this study.

Spathoglottis plicata is a large terrestrial orchid native to Asia Pacific, and has naturalized in various tropical regions of the world including Kenya, West Africa, Hawai'i, Panama, Florida (USA), Cuba, Hispaniola, Puerto Rico, Virgin Islands, and in many of the Lesser Antilles (Catling 1990; Nir 2000; Ackerman 2012a). In Puerto Rico plants have either white or magenta flowers, which are about half the size of *Bletia patula* flowers. The invasive is most commonly found in open and recently disturbed places, such as road cuts (Ackerman 2007). As in many other places where *S. plicata* is naturalized, the flowers are autogamous, fruit set may reach more than 50 % (JDA unpublished), and seed set is approximately 91 % (Dressler 1968; Kores 1979; Ackerman 1995).

Weevil description

Stethobaris polita is a small, black weevil (2.8–3 mm long), native to Puerto Rico, Dominica, Guadeloupe and St. Vincent (O'Brien and Turnbow 2011). Specializing on orchids, adults are florivorous (Wolcott 1948) and lay their eggs in developing fruits and perhaps inflorescence rachises (Light 2011, personal communication). A larger, unidentified weevil was also seen on the flowers but only very rarely.

Study sites

We worked in the northern karst region of Puerto Rico within the municipalities of Isabela (18°26′ N 67°0′W) and Arecibo (18°24′N 66°41′W) where both orchids occur. This region is classified as Subtropical Moist Forest according to the Holdridge Life Zone system, with an annual average precipitation of 1,936 mm and an average temperature of 22 °C (DRNA 2007; Ewel and Whitmore 1973).

Near neighbor analysis

We established two types of plots where *Bletia patula* occurred: one where *S. plicata* was absent and the other where it was present. All plots had the weevil, *Stethobaris polita*. For a year, we monitored 62 individuals of *Bletia patula*, 30 at *S. plicata* absence plots and 32 individuals at *S. plicata* presence plots. We measured the distance to the three nearest flowering *B. patula* and, if present, the distance to the three nearest flowering individuals of *S. plicata*; the average of these distances was used as an index of density. We counted the number of buds, flowers, pollinarium removals and pollinations of target plants, and calculated fruit set of both target and nearest neighbors. The number of weevils (*Stethobaris polita*) was counted on each inflorescence, and the damage they caused was estimated as the percent flower surface area consumed. The damage to flowers was distinctive, and no other florivores were observed. Sample sizes varied among the different measures depending on inflorescence status (e.g., those with only buds will not have data on pollinarium removals).

We analyzed our results using non-parametric statistics. For detecting association between plant densities and data on reproductive effort, reproductive success, weevil abundance and damage, we used Kendall's Tau measure of correlation. For analyzing the differences across treatments (absence or presence of the invader orchid) we used Mann–Whitney U tests.

Choice experiments

We created two types of choice experiments: one where the weevils choose between *B. patula* and magenta *S. plicata* flowers and the other where the weevils choose between *B. patula* and white *S. plicata* flowers. Each choice experiment had two extra combinations in which we exposed the weevils to flowers from the same species (*B. patula* with *B. patula*, *S. plicata* with *S. plicata*); these combinations served as the control groups. Each combination of the choice experiments, including the controls, was done in a petri dish with two flowers and three individuals of *Stethobaris polita*. We repeated each combination twice, and every 24 h for 3 days we assessed the damage done to the flowers using a percent scale. We gave more weight to the column and lip because they are the most important floral parts for pollination and fruit production. Damage scores (0.00–1.00) for each floral part were multiplied by their respective weights (2 for the lip, 3 for the column, and one for each of the sepals and lateral petals). These products were then summed for an overall percent damage score of the flower. The weevils (*S. polita*) were collected from *S. plicata* white and magenta

flower colors and used for the choice experiments that had the same *S. plicata* flower morph. The data were analyzed with a Kruskal–Wallis one-way analysis of variance and for the preference over floral parts we used the Tukey's test for multiple pairwise comparisons.

Distribution maps and patterns of abiotic factors

Distribution maps were created by compiling location data from herbarium records and field surveys (where we collected voucher specimens), resulting in 41 locations for *B. patula* and 43 locations for *S. plicata*. The GPS points where used as presence points in the Maximum entropy algorithm (MaxEnt) to produce the potential distribution of both orchids. In a general way MaxEnt identifies places that share similar environmental factors as that of occurrence points (Phillips et al. 2004). We randomly separated 10 localities as test points for the model and the rest was left as training data, for both orchids. We worked with five bioclimatic data files from Worldclim—Global Climate Data (http://www.worldclim.org/current): annual mean temperature (Bio 01), maximum temperature of warmest month (Bio 05), minimum temperature of coldest month (Bio 06), precipitation of wettest quarter (Bio 16), and precipitation of driest quarter (Bio 17). With these layers and the collection localities we obtained, we ran a model to predict both *B. patula* and *S. plicata* distributions. We also ran models based on the three bioclimatic layers with the highest percent contribution, but our best results for both species were obtained with all five bioclimatic layers. We then determined areas of sympatry as places of possible interaction, assuming the presence of *S. polita*. For this we identified the threshold for equal training of sensitivity and specificity (which MaxEnt generates) and probabilities lower than these thresholds were identified as absence areas for both orchid models. These thresholds allowed us to maintain a more realistic view of what was occurring in Puerto Rico in the context of presence/absence of the species than using an arbitrary threshold such as 0.50 (Liu et al. 2005). Then we multiplied the probability of occurrence of *B. patula* by the probability of occurrence of *S. plicata* obtaining the probability of co-occurrence (sympatry) of the orchids. Finally we determined the area where both species are predicted to coexist.
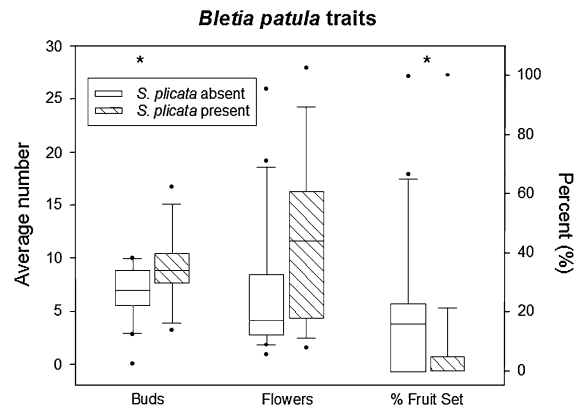

Fig. 1 Reproductive data for *Bletia patula* in Puerto Rico where *Spathoglottis plicata* is absent or present. The sample size for the average number of buds and flowers was 20 in the absence of *S. plicata* and 18 in the presence of *S. plicata*. For the % fruit set the sample size was 19 for both absence and presence of *S. plicata*. We found significant differences when comparing the *S. plicata* absence and present plots for the average number of buds (Mann–Whitney U test: $U = 99$, $z = -2.356$, $P = 0.02$) and the % Fruit Set ($U = 99.5$, $z = -2.754$, $P = 0.003$) of *B. patula*

Results

Near neighbor analysis

The average number of buds produced by *Bletia patula* was higher in plots where *Spathoglottis plicata* co-occurred than where the invasive orchid was absent; there was no significant difference between plots in terms of *B. patula* flower production (Fig. 1). Weevils were more frequent on *B. patula* where *S. plicata* co-occurred (Mann–Whitney U test: $U = 338$, $z = -2.536$, $P = 0.01$), and in such plots percent fruit set in the native orchid was significantly lower (Fig. 1).

Our analyses also revealed a non-significant tendency for *B. patula* flowers to suffer more weevil damage where *S. plicata* co-occurred. Consequently, we suspected that *S. plicata* in low densities might not have any appreciable effect on *B. patula*. We then removed data of four *B. patula* plants from the analyses whose *S. plicata* neighbors averaged more than 2 m distant and found that the total percent average damage to *B. patula* flowers was significantly lower ($P = 0.01$) in *Spathoglottis*-free plots than where the alien orchid was present in high densities (Fig. 2). In this comparison, weevils consumed significantly less *Bletia* sepal, petal, and lip area where

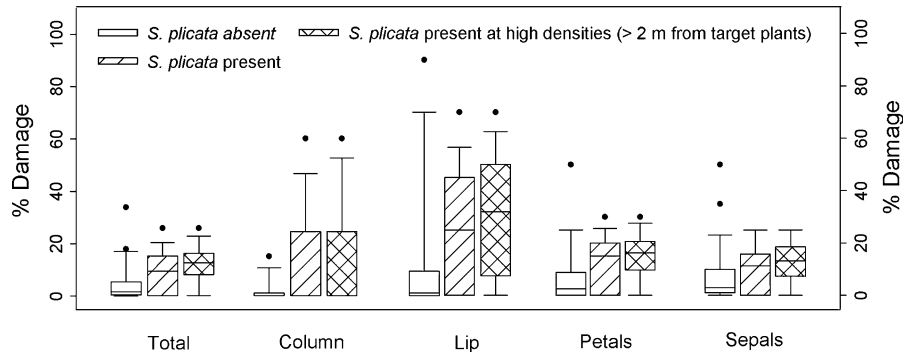## Bletia patula damage to floral traits

Fig. 2 Percent damage to *Bletia patula* floral parts consumed by *Stethobaris polita* where *Spathoglottis plicata* is either present (n = 18) or absent (n = 25). When comparing *S. plicata* absent plots with *S. plicata* present plots (independent of *S. plicata* density index) we found non-significant tendencies for *B. patula* flowers to suffer more weevil damage. When comparing the *S. plicata* absent plots with target plants with high *S. plicata* density index (<2 m from target plant) we found significant differences in the damage created to sepals (Mann–Whitney U test: U = 186.5, z = −0.943, P = 0.02), petals (U = 152.5, z = −1.799, P = 0.01), lip (U = 155.5, z = −1.765, P = 0.02) and total flower damage (U = 161.5, z = −1.558, P = 0.01)

Table 1 Correlations between *Bletia patula* traits (buds, flowers, % fruit set, % damage to flowers and weevils) and average nearest neighbor distances (an index of density) to *B. patula* or *S. plicata*

Measured B. patula traits	All B. patula distances—both sites		S. plicata distance		B. patula distances at S. plicata absence sites		B. patula and S. plicata distances combined	
	Kendall's Tau	p	Kendall's Tau	p	Kendall's Tau	p	Kendall's Tau	p
Buds	−0.15	0.20	−0.26	0.14	−0.01	0.95	−0.22	0.21
Flowers	0.22	0.05	0.05	0.79	0.11	0.49	0.10	0.57
% Fruit set	0.23	0.04	0.18	0.26	0.23	0.15	0.27	0.12
% Damage to flowers	0.03	0.75	−0.32	0.06	0.12	0.39	−0.17	0.33
Weevils	−0.04	0.66	−0.25	0.05	−0.004	0.97	−0.10	0.41

S. plicata was absent. Only damage to the column remained non-significant.

Is reproductive effort, fruit set, weevil numbers and florivory on *Bletia* correlated with *Bletia* or *Spathoglottis* densities? We found that the number of flowers and percent fruit set of *Bletia patula* targets were correlated with the densities of *B. patula*, whereas the number of weevils on *Bletia patula* individuals was correlated with the densities of *S. plicata* (Table 1). Actual damage done by the weevils to *B. patula* flowers had a tendency to vary with *S. plicata* densities, but the test was marginally non-significant (P = 0.06; Table 1). In plots where *S. plicata* was absent, we found that the average number of pollinarium removals in *B. patula* was somewhat higher than where *S. plicata* co-occurred, although the difference

was also non-significant (Mann–Whitney U test: U = 98, z = −1.645, n = 11 with *S. plicata*, n = 25 without *S. plicata*; P = 0.10).

Choice experiments

Weevils collected from *Spathoglottis plicata* flowers in the field will eat both *Spathoglottis* and *Bletia* flowers in the laboratory, and the treatment differences showed the same patterns whether we used white or magenta flowers of *Spathoglottis*. Weevils preferred both magenta *S. plicata* (average damage: 42 %, n = 30) and white *S. plicata* (average damage: 54 %, n = 30) over *B. patula* flowers (Kruskal–Wallis, P = 0.002, DF = 3, χ^2 = 15.30 and P = 0.0001, DF = 3, χ^2 = 25.61 respectively), but *Bletia* still

Table 2 Percent contribution and permutation importance of the five bioclimatic layers used for predicting the distribution of *B. patula* and *S. plicata* in Puerto Rico

B. patula results			*S. plicata* results		
Variable	Percent contribution	Permutation importance	Variable	Percent contribution	Permutation importance
Bio 17	43.2	37.1	Bio 01	35.6	0
Bio 05	24	35.3	Bio 17	25.5	17
Bio 06	22.2	23.4	Bio 16	23	22.6
Bio 16	10.6	4.2	Bio 05	8.4	5.6
Bio 01	0	0	Bio 06	7.4	54.9

Bio 01 = annual mean temperature; Bio 05 = maximum temperature of warmest month; Bio 06 = minimum temperature of coldest month; Bio 16 = precipitation of wettest quarter; Bio 17 = precipitation of driest quarter. The top three for each species were used for the corresponding species distribution model

Table 3 Areas under the curve (AUC) from MaxEnt runs of training, test and random prediction for *Bletia patula* and *Spathoglottis plicata* using all five layers and only the three layers with highest percent contribution (see Table 2)

AUC	*B. patula* model		*S. plicata* model	
	Using 5 layers	Using 3 layers	Using 5 layers	Using 3 layers
Training	0.893	0.756	0.913	0.879
Test	0.935	0.742	0.903	0.886
Random prediction	0.5	0.5	0.5	0.5

suffered considerable damage in the presence of either magenta *S. plicata* (average damage: 30 %, n = 30) or white *S. plicata* (average damage: 28 %, n = 30). Weevils on the *Bletia* (from both magenta and white *S. plicata*) mostly ate petals and lip area (Tukey's test for multiple pairwise comparisons, weevils from magenta *Spathoglottis*, P = 0.001, n = 30, & weevils from white *Spathoglottis*, P = 0.0004, n = 30).

Distribution maps and patterns of abiotic factors

The three layers with the highest percent contribution to the area under the curve (AUC) varied among species (Table 2). The AUCs for both the training and the test data were highest when we used all five layers (Table 3). This was true for both *Bletia patula* and *Spathoglottis plicata* models. Because we wanted to predict where *B. patula* and *S. plicata* might be sympatric, we used all five layers to obtain the most

reliable distribution for detecting regions of sympatry. The threshold for equal training of sensitivity and specificity gave 0.40 and 0.48 for *S. plicata* and *B. patula*, respectively. After multiplying the probability of *B. patula* and *S. plicata* we obtained different probabilities and size patches in different regions of the island (Fig. 3c). The current distribution of the native *B. patula* is nearly limited to the northern karstic region of Puerto Rico (Fig. 3a). The naturalized *S. plicata* has a broader range and the models predict that its distribution will strongly overlap with that of *B. patula* (Fig. 3b, c).

Discussion

We documented the effect of the florivorous weevil, *Stethobaris polita*, on the native orchid, *Bletia patula*, in the presence and absence of an additional food source, the invasive orchid, *Spathoglottis plicata*. Wherever *S. plicata* was nearby, weevils were more common on *Bletia*, flower production was reduced, and fruit set suffered. In fact, there was a positive relationship between *S. plicata* densities and both the number of weevils on *Bletia* and the amount of *B. patula* flower damage. Our results are analogous to other studies where an increment in prey leads to higher predator populations negatively affecting other prey in the area (Schmitt 1987; Rand 2003; White et al. 2006; Orrock et al. 2008). Thus, we propose that apparent competition occurs between *S. plicata* and *B. patula* orchids, and is mediated by the florivorous weevil *S. polita*.
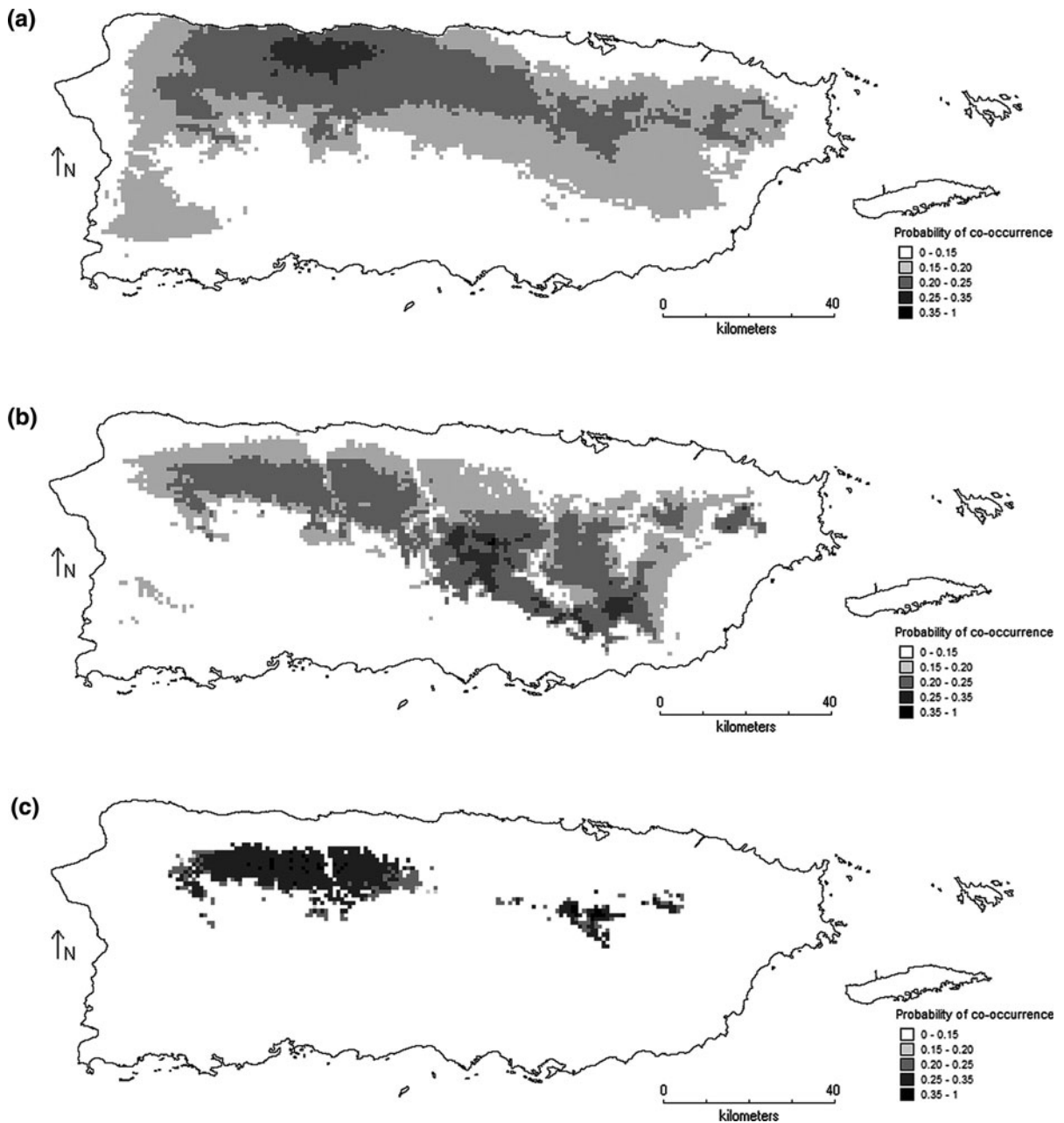
Fig. 3 Predicted distribution based on five environmental layers using the MaxEnt algorithm for species distribution modeling for **a** *Bletia patula*, **b** *Spathoglottis plicata* and **c** the probability of the co-occurrence of *B. patula* and *S. plicata*, utilizing the threshold for equal sensitivity and specificity to determine areas of no occurrence. For the probability of co-occurrence of *B. patula* and *S. plicata* the range of probabilities from 0 to 0.15 cover an area of 9,789 km^2, probabilities from 0.15 to 0.20 cover 6 km^2, probabilities from 0.20 to 0.25 cover 148 km^2, probabilities from 0.25 to 0.35 cover 510 km^2, and probabilities from 0.35 to 1 cover 33 km^2 of the island

The damage adult *Stethobaris* inflicts on flowers may reduce their attractiveness to pollinators resulting in the lower fruit production we had observed in *Bletia*

patula. Other species of *Stethobaris* are known to specialize on orchid flowers and also oviposit in their developing fruits causing substantial seed loss through

predation and secondarily through bacterial or fungal infections (Sieg 1993; St. Hilaire 2002; Light and Macconaill 2011). We often observed larvae in fruits of *Spathoglottis* and found that severely infected fruits often abort before dehiscence. When fruits abort in *Bletia*, they do so within a week before our next census so we have not yet confirmed that such fruits are infected with larvae.

Natural fruit set in *Bletia patula* is relatively low compared to rewarding species, a phenomenon commonly associated with the deception pollination system that they employ (Ackerman 1986; Ackerman and Carromero 2005; Tremblay et al. 2005). The advantages of such a system continue to be investigated (Montalvo and Ackerman 1987; Nilsson 1992; Meléndez-Ackerman et al. 2000; Johnson et al. 2004; Smithson 2002, 2005) but to these arguments we can add that low fruit set may reduce apparency to seed predators. The addition of flowering *Spathoglottis* in the neighborhood of *B. patula* not only adds floral resources for adult weevils, but the selfing flowers of these invasive orchids may also substantially increase fruit and seed resources for their larvae with negative consequences for *B. patula*. Indeed, in other plants increased pollination resulting in higher fruit set can increase fruit or seed predation (Cariveau et al. 2004; Strauss and Irwin 2004), and under certain circumstances seed predators may have a greater influence on floral trait selection than pollinators (Parachnowitsch and Caruso 2008).

Paradoxically, we found where *Bletia* occurred with *Spathoglottis*, bud production was higher but flower production was not statistically different. We suspect *Bletia patula* selectively aborts buds with weevil damage. Since orchid inflorescences are indeterminate, bud development can be adjusted depending on resource availability (Ackerman 1989). By aborting damaged buds, resources can be reallocated to produce more buds. Ultimately, plants that suffered bud damage and bud abortions still produced the same number of open flowers.

Given a choice, weevils will eat more of *Spathoglottis plicata* flowers than of *Bletia patula*. The damage they do to *B. patula* may be a consequence of spillover, even though this species is one of the weevil's natural food items. Unlike *S. plicata*, *B. patula* depends on pollinator service for reproduction. The weevils would eat any floral part of *B. patula*, but most damage was done to petals and the lip.

Although we did not experimentally manipulate plants in the field, plots with high density of *Spathoglottis* had more weevils, more floral damage, and less fruit production on *B. patula* than plots with few or no *Spathoglottis* suggesting that the weevils play a significant role in reproductive success of *B. patula*. The weevils may affect fitness through altering floral attractiveness; and we did find a non-significant tendency ($P = 0.1$) for reduced frequency in pollinarium removals whenever *S. plicata* was present. However, experimental studies have failed to find such a relationship in other orchids (Malo et al. 2001; Cuartas-Domínguez and Medel 2010). Alternatively, the reduced fruit set in *Bletia* may be a consequence of weevils ovipositing in developing ovaries causing abortions.

Our species distribution modeling showed that the northern karstic region has the highest probability of co-occurrence of the two orchid species. We expected this pattern since nearly all known localities of *Bletia patula* are from this region, whereas *Spathoglottis plicata* can be found in almost any moist region of Puerto Rico, from near sea level to the dwarf cloud forests of the highest elevations. If our observations of apparent competition are consistent wherever the two orchids co-occur, then we expect the seed-limited *B. patula* populations to gradually decline until weevils either become sparse or *Bletia* becomes less apparent to them.

Naturalized, invasive orchids are largely ignored as potentially significant elements of floras (but see Bonnardeaux et al. 2007) and may even be appreciated for their esthetic values as some have quite showy flowers and are often visible in disturbed areas such as roadsides (Ackerman 2012b). Although it is unlikely that they will have the impact on natural ecosystems as have many other invasive plant species (Lowe et al. 2000), we have shown that in the case of *Spathoglottis plicata* in Puerto Rico, they can have subtle effects by raising the abundance of native florivorous weevils to pest levels resulting in an indirect negative effect on populations of native orchids.

References

Ackerman JD (1986) Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1:108–113

Ackerman JD (1989) Limitations to sexual reproduction in *Encyclia krugii* (Orchidaceae). Syst Bot 14:101–109. doi:10.2307/2419054

Ackerman JD (1995) An orchid flora of Puerto Rico and the Virgin Islands. Mem New York Bot Gard 73:1–203

Ackerman JD (2007) Invasive orchids: weeds we hate to love? Lankesteriana 7:19–21

Ackerman JD (2012a) Orchidaceae. In: Acevedo P, Strong M (eds) Catalogue of seed plants of the West Indies. Smithsonian Contrib Bot 98: 622–667. http://hdl.handle.net/10088/17551

Ackerman JD (2012b) Orchids gone wild: discovering naturalized orchids in Hawaii. Orchids 81:88–93

Ackerman JD, Carromero W (2005) Is reproductive success related to color polymorphism in a deception pollinated tropical terrestrial orchid? Caribb J Sci 41:234–242

Ackerman JD, Sabat A, Zimmerman JK (1996) Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. Oecologia 106:192–198. doi:10.1007/BF00328598

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. Annu Rev Ecol Evol Syst 40:1–20. doi:10.1146/annurev.ecolsys.110308.120242

Bonnardeaux Y, Brundrett M, Batty A, Dixon K, Koch J, Sivasithamparam K (2007) Diversity of mycorrhizal fungi of terrestrial orchids: compatibility web, brief encounters, lasting relationships and alien invasions. Mycol Res 111:51–61. doi:10.1016/j.mycres.2006.11.006

Calvo RN, Horvitz C (1990) Pollinator limitation, cost of reproduction, and fitness in plants: transition matrix demographic approach. Am Nat 136:499–516. doi:10.1086/285110

Cariveau D, Irwin RE, Brody AK, García Mayeya L, von der Ohe A (2004) Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. Oikos 104:15–26. doi:10.1111/j.0030-1299.2004.12641.x

Catling PM (1990) Auto-pollination in the Orchidaceae. In: Arditti J (ed) Orchid biology: reviews and perspectives. V. Timber Press, Portland, pp 121–158

Cuartas-Domínguez M, Medel R (2010) Pollinator-mediated selection and experimental manipulation of the flower phenotype in *Chloraea bletioides*. Funct Ecol 24:1219–1227. doi:10.1111/j.1365-2435.2010.01737.x

Daehler CC (2006) Invasibility of tropical islands by introduced plants: partitioning the influence of isolation and propagule pressure. Preslia 78:389–404

Darwin CR (1877) The various contrivances by which orchids are fertilized by insects, 2nd edn. John Murray, London

Departamento de Recursos Naturales y Ambientales (DRNA), Estado Libre Asociado de Puerto Rico (2007) Bosques de Puerto Rico: El Bosque de Río Abajo. Hojas de nuestro ambiente. P-023. http://www.drna.gobierno.pr/biblioteca/publicaciones/hojas-de-nuestro-ambiente/23-Rio%20Abajo.pdf. Accessed 24 Aug 2011

Dressler RL (1968) Notes on *Bletia* (Orchidaceae). Brittonia 20:182–190

Dressler RL (1981) The orchids: natural history and classification. Harvard University Press, Cambridge Mass

Ewel JJ, Whitmore JL (1973) The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Forest service research paper ITF-18, Department of Agriculture and Institute of Tropical Forestry, Forest Service, US

Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol Appl 8:975–989. doi:10.1890/1051-0761(1998)008[0975:EOINIP]2.0.CO;2

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229

Holt RD, Hochberg ME (2001) Indirect interactions, community modules and biological control: a theoretical perspective. In: Wajnberg E, Scott JK, Quimby PC (eds) Evaluating indirect ecological effects of biological control, 1st edn. CABI, New York, pp 13–38

Hoogendoorn M, Heimpel GE (2002) Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. Biol Control 25:224–230. doi:10.1016/S1049-9644(02)00101-9

Johnson SD, Peter CI, Agren J (2004) The effects of nectar addition on pollen removal and geitonogamy in the non-rewarding orchid, *Anacamptis morio*. Proc R Soc Lond B-Biol Sci 271:803–809. doi:10.1098/rspb.2003.2659

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Eco Evol 17:164–170. doi:10.1016/S0169-5347(02)02499-0

Kores PJ (1979) Taxonomy and pollination in the wild Hawaiian orchids. M.S. Thesis, University of Hawai'i, Manoa

Kueffer C, Daehler CC, Torres-Santana CW, Lavergne C, Meyer J, Otto R, Silva L (2010) A global comparison of plant invasions on oceanic islands. Perspect Plant Ecol Evol Syst 12:145–161. doi:10.1016/j.ppees.2009.06.002

Lau JA, Strauss SY (2005) Insect herbivores drive important indirect effects of exotic plants on native communities. Ecology 86:2990–2997. doi:10.1890/04-1779

Leavitt H, Robertson IC (2006) Petal herbivory by chrysomelid beetles (*Phyllotreta* sp.) is detrimental to pollination and seed production in *Lepidium papilliferum* (Brassicaceae). Ecol Entomol 31:657–660. doi:10.1111/j.1365-2311.2006.00820.x

Light MHS, Macconaill M (2011) Potential impact of insect herbivores on orchid conservation. Euro J Environ Sci 1:115–124

Liu C, Berry PM, Dawson TP, Pearson R (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393. doi:10.1111/j.0906-7590.2005.03957.x

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology, 2nd edn. Blackwell, London

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species. A selection from the global invasive species database. Invasive Species Specialist Group, Species Survival Commission, International Union for Conservation of Nature, Aukland

Malo JE, Leirana-Alcocer J, Parra-Tabla V (2001) Population fragmentation, florivory, and the effects of flower morphology alterations on the pollination success of *Myrmecophila tibicinis* (Orchidaceae). Biotropica 33:529–534. doi:10.1646/0006-3606(2001)033[0529:PFFATE]2.0.CO;2

McCall AC (2008) Florivory affects pollinator visitation and female fitness in *Nemophila menziesii*. Oecologia 155:729–737. doi:10.1007/s00442-007-0934-5

McCall AC, Irwin RE (2006) Florivory: the intersection of pollination and herbivory. Ecol Lett 9:1351–1365. doi:10.1111/j.1461-0248.2006.00975.x

Meléndez-Ackerman EJ, Ackerman JD, Rodríguez-Robles JA (2000) Reproduction in an orchid can be resource-limited over its lifetime. Biotropica 32:282–290. doi:10.1646/0006-3606(2000)032[0282:RIAOCB]2.0.CO;2

Montalvo AM, Ackerman JD (1987) Limitations to natural fruit production in *Ionopsis utricularioides* (Orchidaceae). Biotropica 19:24–31

Nilsson LA (1992) Orchid pollination biology. Trends Ecol Evol 7:255–258. doi:10.1016/0169-5347(92)90170-G

Nir M (2000) Orchidaceae Antillanae. DAG Media Publishing, New York

Noonburg EG, Byers JE (2005) More harm than good: when invader vulnerability to predators enhances impact on native species. Ecology 86:2555–2560. doi:10.1890/05-0143

O'Brien CW, Turnbow RH Jr (2011) An annotated list of Curculionidae (Coleoptera) of Dominica (excluding Scolytinae and Platypodidae). Insecta Mundi 0179:1–31

Orrock JL, Witter MS, Reichman OJ (2008) Apparent competition with an exotic plant reduces native plant establishment. Ecology 89:1168–1174. doi:10.1890/07-0223.1

Parachnowitsch AL, Caruso CM (2008) Predispersal seed herbivores, not pollinators, exert selection on floral traits via female fitness. Ecology 89:1802–1810. doi:10.1890/07-0555.1

Phillips SJ, Dudik M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In: Proceedings of the 21st international conference on machine learning, Banff, Canada

Rand TA (2003) Herbivore-mediated apparent competition between two salt marsh forbs. Ecology 84:1517–1526. doi:10.1890/0012-9658(2003)084[1517:HACBTS]2.0.CO;2

Rand TA, Louda SM (2004) Exotic weed invasion increases the susceptibility of native plants to attack by a biocontrol herbivore. Ecology 85:1548–1554. doi:10.1890/03-3067

Ricciardi A (2001) Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Can J Fish Aquat Sci 58:2513–2525. doi:10.1139/cjfas-58-12-2513

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107. doi:10.1046/j.1472-4642.2000.00083.x

Russell FL, Louda SM (2005) Indirect interaction between two native thistles mediated by an invasive exotic floral herbivore. Oecologia 146:373–384. doi:10.1007/s00442-005-0204-3

Russell FL, Louda SM, Rand TA, Kachman SD (2007) Variation in herbivore-mediated indirect effects of an invasive plant on a native plant. Ecology 88:413–423. doi:10.1890/0012-9658(2007)88[413:VIHIEO]2.0.CO;2

Schmitt RJ (1987) Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. Ecology 68:1887–1897. doi:10.2307/1939880

Sheppard AW, van Klinken RD, Heard TA (2005) Scientific advances in the analysis of direct risks of weed biological control agents to nontarget plants. Biol Control 35:215–226. doi:10.1016/j.biocontrol.2005.05.010

Sieg CH (1993) *Stethobaris commixta* Blatchley (Coleoptera: Curculionidae) collected from a species of orchid, *Platanthera praeclara* Sheviak and Bowles in North Dakota tall-grass prairie. Prairie Nat 25:81

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102. doi:10.1146/annurev.ecolsys.110308.120304

Simberloff D, Von Hollen B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32. doi:10.1023/A:1010086329619

Smithson A (2002) The consequences of rewardlessness in orchids: reward-supplementation experiments with *Anacamptis morio* (Orchidaceae). Am J Bot 89:1579–1587. doi:10.3732/ajb.89.10.1579

Smithson A (2005) Pollinator limitation and inbreeding depression in orchid species with and without nectar rewards. New Phytol 169:419–430. doi:10.1111/j.1469-8137.2005.01592.x

St. Hilaire L (2002) *Amerorchis rotundifolia* (Banks ex Pursh) Hultén, small round-leaved *Orchis*. Conservation and Research Plan for New England. New England Conservation Program, Framingham, MA, p 48

Strauss SY (1991) Indirect effects in community ecology: their definition study and importance. Trends Ecol Evol 6:206–210. doi:10.1016/0169-5347(91)90023-Q

Strauss SY, Irwin RE (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. Annu Rev Ecol Evol Syst 35:435–466. doi:10.1146/annurev.ecolsys.35.112202.130215

Strauss SY, Irwin RE, Lambrix VM (2004) Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. J Ecol 92:132–141. doi:10.1111/j.1365-2745.2004.00843.x

Tremblay RL, Ackerman JD, Zimmerman JK, Calvo RN (2005) Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biol J Linn Soc 84:1–54. doi:10.1111/j.1095-8312.2004.00400.x

Trethowan PD, Robertson MP, McConnachie AJ (2011) Ecological niche modelling of an invasive alien plant and its potential biological control agents. S Afr J Bot 77:137–146. doi:10.1016/j.sajb.2010.07.007

van der Pijl L, Dodson CH (1966) Orchid flowers: their pollination and evolution. University of Miami Press, Coral Gables, FL

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. Divers Distrib 12:443–455. doi:10.1111/j.1366-9516.2006.00265.x

Wiggins GJ, Grant JF, Lambdin PL, Ranney JW, Wilkerson JB, VanManen FT (2010) Spatial prediction of habitat overlap of introduced and native thistles to identify potential areas of nontarget activity of biological control agents. Environ Entomol 39:1866–1877. doi:10.1603/EN10112

Wolcott GN (1948) The insects of Puerto Rico. Coleoptera. J Agric Univ Puerto Rico 32:225–416