

# Present and Future Distribution of Two Non-Indigenous Orchids and Their Acquired Enemy in Puerto Rico

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## Research Article

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## Abstract

Establishment of new populations is contingent on overcoming abiotic and biotic barriers. While this applies to all species, these hurdles are at the forefront of invasion biology where prediction, prevention, eradication, and control strategies depend on an understanding of these processes. *Arundina graminifolia* and *Dendrobium crumenatum* are two non-indigenous orchids spreading throughout Puerto Rico. The two species have acquired a native herbivore & seed predator, the orchid-specialist weevil, *Stethobaris polita*. With recently acquired presence records of the three species, land cover data and BioClim variables, we modeled their potential distributions under current conditions and also those projected under the least and most extreme climate scenarios for 2050 and 2070. We show that *D. crumenatum* flourishes in urban environments which also provide refugia from *S. polita*, whereas there is currently limited refugia for *A. graminifolia* from *S. polita* attack, as this orchid is sensitive to the same climatic variables as the weevil. Projections into all climate scenarios suggest range retractions for all species, with an equal to or greater proportion of both orchid populations subject to *S. polita* attack. Thus, we illustrate for island invasions how climate change will likely alter the distribution of acquired biotic interactions.

## Introduction

Over the past century, our natural world has dealt with new, largely human-induced changes at an unprecedented rate and scale. Increasingly obvious are the changes brought about by biological invasions which have become relentlessly pervasive worldwide (Stohlgren et al. 2008; Seebens et al. 2017). Islands are particularly susceptible to invasions (D'Antonio and Dudley 1995; Denslow et al. 2009; Pulwarty et al. 2010; but see Jeschke et al. 2012), where some impacts vary from positive to negative, and obvious and dramatic to subtle and unexpected (e.g., Vitousek and Walker 1989; O'Dowd et al. 2003; Sin et al. 2008; Abelleira Martínez et al. 2010; Recart et al. 2013). In Puerto Rico, barrages of invasive species are being introduced including greater numbers of non-native orchids (e.g., Rojas-Sandoval and Acevedo-Rodríguez 2015; Falcón and Tremblay 2018; Ackerman 2007, 2017). Although orchids are disproportionately underrepresented among invasive species (Daehler 1998), they can have both positive and negative impacts (e.g., apparent competition, Recart et al. 2013). For this reason, it is important to identify recent invasions and factors associated with their establishment, spread and consequences to invaded communities.

Upon introduction, invaders immediately interact with the local biological community, and the interactions they acquire can have dramatic consequences for invasion dynamics. Whether positive or negative, they can heavily influence the rate of spread and population health of invasive species (de Araújo et al. 2014; Svenning et al. 2014). Upon departure from home ranges, alien species usually leave their enemies behind which may enhance invasion success through processes involving enemy release (Shea and Chesson 2002; Allendorf and Lundquist 2003; Fagan et al. 2005). On the other hand, the acquisition of negative interactions may hamper or even prevent invasion success providing some degree of biotic resistance (Elton 1958; Thompson et al. 2007; Falcón et al. 2017). Yet the lack of shared evolutionary history between invaders and acquired enemies should prevent these interactions from being spatially homogenous across environmental gradients (Fine et al. 2004). In this way, identifying areas of refuge from acquired enemies is an integral part of accurately predicting invasive spread.

Natural habitat heterogeneity is normal, but human activities such as urbanization disturb environments well beyond what native species generally experience, creating opportunities for pre-adapted, non-indigenous species (Daehler 2003). The divergent abilities among native and exotic species to adjust to urbanized worlds can create refuge from biotic resistance. Indeed, urban areas facilitate non-native prominence by weakening any biotic resistance of native species (Holway 1995; Vila and Pujadas 2001; Burton et al. 2005; McKinney 2006; Soifer and Ackerman 2019).

Besides overlaying the more obvious local effects of human activities on environmental conditions, regional climate change may also affect dynamics of invasions, especially along the leading and trailing edges of an invasion front (Van der Putten et al. 2010; Hillerislambers et al. 2013; Lankau et al. 2015). These changes are expected to alter current species distributions, either through latitudinal/altitudinal shifts, range expansions or contractions (Walther et al. 2002) and the responses are likely to vary among species, altering the outcome of species interactions (Menéndez et al. 2008). In this way, climate change might create or eliminate areas of refuge, while also ameliorating or exacerbating rates of spread in new territories.

Herein we focus on populations of *Arundina graminifolia* (bamboo orchid) and *Dendrobium crumenatum* (pigeon orchid), two species native to tropical and subtropical Asia and adjacent islands that are now well-established in Puerto Rico. As both invasions are actively spreading across the island from east to west, understanding their fullest possible extent ahead of time can provide useful information for future research and/or mitigation efforts on either species.

While modelling distributions and recording climatic responses, it is important to contextualize both invasions with their known ecological interactions and with the impending changes in the current climate system. Both invasive orchids have acquired a new enemy in the form of the native herbivore and seed predator, *Stethobaris polita*, an orchid-specialist weevil known to compromise fruit set and seed production resulting in strong demographic effects on its hosts (Recart et al. 2013; Falcón et al. 2017). The implications of this interaction for both

species on the island has not been quantified; however, the introduction of additional exotic orchids may increase risk to native orchids through apparent competition (Recart et al. 2013). In this way, understanding the extent of these interactions with *S. polita* across the island can also be particularly useful in understanding their greater ecological impacts.

Species distribution models (SDM) are frequently utilized to project species range shifts under climate change, and recently, they have been used to predict distribution differences between interacting species. Most such studies focus on mutualistic relationships (e.g. plant-pollinator) (Kolanowska and Jakubska-Busse, 2020; Malekia and Sadeghi, 2020), while fewer examine how climate change will influence the scale of negative biotic interactions (Menéndez et al. 2008; Aryal et al. 2016).

Herein, we investigate the current spatial extent of both orchid invasions while identifying areas of refuge from weevil attack. Additionally, we explore how the distributions of all three species, along with the extent of their interactions, might shift under future climate change scenarios. We anticipate the lowland *D. crumenatum* to exhibit an upward altitudinal range shift, increasing the geographical extent of interactions with *S. polita*, while the highland *A. graminifolia* will likely exhibit a range contraction under climate change, possibly creating a natural mitigation for the invasion on the island.

## Materials And Methods

### Study Species

Current knowledge on both species in Puerto Rico, beyond herbarium collections, is rather sparse. The first naturalized population of *A. graminifolia* was discovered in Río Grande, Puerto Rico, a few kilometers from an orchid nursery that had a cluster of them on their grounds, so it is likely they arrived via the horticultural trade as has happened elsewhere (Ackerman 1995, 2012). The first recorded naturalized population of *D. crumenatum* was discovered in 2005 growing on *Annona glabra* (Annonaceae) in the Sabana Seca marsh, Municipality of Toa Baja (Ackerman and Collaborators 2014). Since their original discoveries, both populations have spread across the island, as evidenced by local herbarium records (<http://herbario.uprrp.edu/>, accessed 19 Jun 2019).

Both orchid species exhibit signs of high climate sensitivity, making their responses to climate change particularly important in modelling their distributions. *Arundina graminifolia* is found naturalized at higher elevations, indicating a sensitivity to higher temperatures. Previous research has established that under any climate change scenario, habitat suitability declines globally for *A. graminifolia*, although the specific implications for this loss are unknown for Puerto Rico (Kolanowski and Konowalik 2014).

The potential distribution of the epiphytic *D. crumenatum* or its response to climate change has not been modeled. However, a strong – and perhaps unusual – climatic response may be expected for *D. crumenatum* because epiphytes, which by virtue of being exposed to the elements, are especially susceptible to vagaries of weather (Benzing 1990; Zotz 2016). The gregarious flowering of *D. crumenatum* is triggered by rain-induced temperature drops (Brooks and Hewitt 1909; Seifríz 1923; Goh et al. 1982). Changes in the frequency of these temperature drops may influence habitat suitability for *D. crumenatum*. For current distribution models of *D. crumenatum* to remain applicable in the coming decades, they must account for scenarios with an altered climate.

*Stethobaris polita* is not known to inhabit urban landscapes, either due to an inability to disperse into or establish within such environments (Soifer and Ackerman 2019). The weevils' absence in urban areas enables orchids, such as *D. crumenatum*, to escape herbivore attack and quickly establish populations. Such refugia have been observed for *Spathoglottis plicata*, another non-native, invasive orchid in Puerto Rico (Soifer and Ackerman 2019). *Arundina graminifolia* is found at higher elevations than the current urban extent; however, there may be other environmental barriers providing refugia from *S. polita* attack, such as seasonal temperature or precipitation levels.

### Study Site

During June and July 2019, we crisscrossed the Caribbean island of Puerto Rico (18.2208° N, 66.5901° W) searching for *Arundina graminifolia* and *Dendrobium crumenatum*. Puerto Rico has six Holdridge Life Zones: subtropical dry forest, subtropical moist forest, subtropical wet forest, subtropical rainforest, subtropical lower montane wet forest, and subtropical lower montane rain forest (Ewel and Whitmore 1973). We covered all but the dry forest habitats which are not known to harbor either orchid species or the weevil.

### Collection of Occurrence Records

We obtained coordinates using Garmin eTrex® GPS and recorded plant data for populations along trails and roadsides, and on public and private properties. The locations of individual populations were obtained from herbarium collections and personal communications. Some populations were also identified through incidental discovery, either during travels between known populations, or through intentional scouting in previously unexplored municipalities. We collected population data from the following 19 municipalities: Adjuntas, Aibonito,

Barranquitas, Caguas, Canóvanas, Carolina, Cayey, Cidra, Jayuya, Lares, Luquillo, Naranjito, Orocovis, Patillas, Río Grande, San Juan, San Sebastian, Trujillo Alto, and Utuado.

Populations were only considered if there was evidence of naturalization and/or recruitment as follows: the presence of reproductive structures (flowers or fruits) on at least one plant; the presence of recruits in the population; or sufficient circumstantial evidence that the population was not cultivated, such as the plant being inaccessible to the general public (i.e. on top of a steep roadside hill or high up a tree). Even if a population was originally cultivated, it was still included if successful recruitment was evident, acknowledging the role of the horticultural trade as a vector in non-native orchid dispersal.

At every population, we recorded the number of *S. polita* present, along with the presence of other possible enemies. We categorized weevil presence at a waypoint from either weevil sightings or evidence of weevil damaged reproductive structures (buds, flowers, fruits).

Samples included a total of 30 populations of *D. crumenatum*, 28 populations of *A. graminifolia*, and 140 populations of *S. polita*. Since presence points for *S. polita* would be limited to the presence points of our two orchids, their modelled distribution might create an incomplete picture of their overall distribution. To counteract this issue, we combined our *S. polita* presence points with those recorded with a more widespread alien orchid, *Spathoglottis plicata* (Recart et al. 2013; Soifer and Ackerman 2019). For this reason, the number of populations of *S. polita* is higher than those of either orchid.

#### Distribution modelling and mapping

We modelled the distributions of *A. graminifolia*, *D. crumenatum* and *S. polita* using Maxent v 3.4.1 (Phillips et al. 2019), similar to previous studies on invasive species distribution in both the present and future (Recart et al. 2013; Kolanowska and Konowalik 2014; Soifer and Ackerman 2019). We used ten environmental layers, including eight bioclimatic layers from Worldclim Version 2--Global Climate Data (Fick and Hijmans 2017), elevation and land cover (PRGAP 2006). The climatic layers chosen were based on similar studies for the same study species, or within the same study area: annual mean temperature (Bio 01), temperature seasonality (Bio 04), maximum temperature of warmest month (Bio 05), minimum temperature of warmest month (Bio 06), mean temperature of driest quarter (Bio 09), precipitation seasonality (Bio 15), precipitation of wettest quarter (Bio 16), and precipitation of driest quarter (Bio 17) (Soifer and Ackerman 2019; Kolanowska and Konowalik 2014; Recart et al. 2013). Bioclimatic variables and elevation had a spatial resolution of 30 arc-seconds (~ 1 km) and land cover had a resolution of 15 m<sup>2</sup> (Gould et al. 2008). We prepared the environmental layers for Maxent on ArcGIS with the Extract By Mask tool with the "Convert Units" setting to match the extent, cell size, and coordinate system of the PRGAP land cover map. All layers had a final resolution of 15 m<sup>2</sup> and the coordinate system NAD 1983 Stateplane Puerto Rico Virgin Islands FIPS 5200.

We ran maxent models for *A. graminifolia*, *D. crumenatum*, and *S. polita* with 10-fold cross-validation to estimate error around the mean model, which has been identified as a reliable method for projecting onto novel climate scenarios (Elith et al. 2010), logistic output, and the remaining default settings. For any cell with more than one population, only one was used to contribute to the model. This resulted in only 84 of the 140 *S. polita* populations contributing to the models.

We applied the threshold rule of equal training sensitivity and specificity similar to previous studies (Soifer and Ackerman 2019) to produce binary presence/absence maps in ArcGIS, with cells below the calculated threshold marked as 0, and cells above threshold for each species marked in a unique number (1, 2 or 4). Cells that were above the threshold for multiple species were marked as the sum of their corresponding numbers. Comparisons across models quantified range shifts and range overlap under climate change.

Using the same variables and settings, along with clamping, we projected the distribution of the three species into 2050 and 2070 using the general circulation models (GCM), CCSM4 (Community Climate System Model 4) and CNRM-CM5 (Centre National de Recherches Météorologiques-Coupled Model 5), across representative concentration pathways (RCP) 2.6 and 8.5 (Fick and Hijmans 2019). GCMs were chosen based on their use in similar studies (Malekian and Sadeghi, 2019; Kolanowska and Jakubka-Busse, 2020; Tsiftsis and Djordjević, 2020).

Variation among individual GCMs brings into question how accurate any single GCM is for a particular area (Goberville et al. 2015). For example, Khalyana et al. (2016) found that model recognition of Puerto Rico's bimodal precipitation patterns strongly affected climate projections for the island, with bimodal models projecting more severe climate change than unimodal models. While there is no "best" model to use for Puerto Rico, previous studies have used multiple GCMs to account for some of the variation in GCM outputs (Goberville et al. 2015; Dyderski et al. 2018). For this reason, we used one GCM (CNRM-CM5) that models bimodal precipitation patterns, and another GCM (CCSM4) that is unimodal for the Caribbean (Hayhoe, 2013). In doing so, we anticipated having one model (CCSM4) provide more conservative projections than the other (CNRM-CM5), accounting for GCM variation. Doing so also tested the consistency of observed patterns against GCM variability.

## Model evaluation

Along with modelling species distributions, Maxent provides multiple statistical tests on model significance and performance. We used the area under the receiver operating characteristic curve (AUC) to discern model output from a random prediction. We conducted jackknife tests to evaluate variable importance.

## Results

Present and potential species distributions and interactions based on current conditions

Field observations confirm that both *A. graminifolia* and *D. crumenatum* have acquired a new enemy, *S. polita*. We found the weevil more often on *A. graminifolia* than *D. crumenatum*. Of the 30 populations of *D. crumenatum* surveyed, only 6 contained evidence of *S. polita* damage. In comparison, 20 of the 28 *A. graminifolia* populations surveyed had evidence of *S. polita* damage to their sepals, lip, and/or petals, including oviposition in *A. graminifolia* fruits. Although *S. polita* has been seen feeding on meristematic tissue of *D. crumenatum* in the absence of flowers (JDA personal observations), we observed weevils during sporadic flowering events, with similar damage to *D. crumenatum* flowers as observed on *A. graminifolia*. Ovipositing holes in fruits of *D. crumenatum* were observed as well.

The average AUC values for each species indicate the following model fits (*S. polita*: AUC =  $0.885 \pm 0.061$ ; *D. crumenatum*: AUC =  $0.915 \pm 0.031$ ; *A. graminifolia*: AUC =  $0.922 \pm 0.076$ ) (Fig. S1). After applying an equal training sensitivity and specificity threshold, average presence thresholds varied among taxa: *S. polita*, *D. crumenatum*, and *A. graminifolia* (0.1834, 0.3345 and 0.2458, respectively).

For *A. graminifolia*, Maxent predicts suitable habitat within the higher elevations of the Cordillera Central, Carite Forest and El Yunque National Forest, which matches our field observations of population occurrence (Fig. 1a). Jackknife tests reveal temperature variables, along with elevation, largely determine *A. graminifolia* presence (Fig. S2a). Response curves for *A. graminifolia* to these variables reveal an affinity for lower temperatures, and the lower altitudinal extent of *A. graminifolia* is roughly 500 m (Fig. S3).

For *D. crumenatum*, our models show an affinity towards areas of urban development with suitable habitat coinciding with urban areas, particularly San Juan and the Caguas-Cayey region, which is where we observed high densities of *D. crumenatum* populations (Fig. 1b). *Dendrobium crumematum* appears to prefer lower elevations and largely disturbed habitat, while being potentially absent from El Yunque National Forest and Cordillera Central. The model is largely influenced by land cover, as the AUC is higher with land cover alone than when it is excluded (Fig. S2b). However, areas of high human land use are not the sole variable necessary for survival. Jackknife tests also reveal precipitation and temperature seasonality, precipitation during the wettest and driest quarter, and mean temperature influence the model (Fig. S2b). Response curves reveal an affinity towards areas with year-round precipitation at high levels, but also areas with high temperatures and high seasonality in temperature (Fig. S4). As a result, the dry habitats on the south side of the island remain largely uninhabitable, even within large urban areas like Ponce (Fig. 1b).

For *S. polita*, our models show a negative relationship with urban land cover. The intact forests of El Yunque and Carite are deemed the most suitable habitat, with hot spots projected in those areas (Fig. 1c). At the same time, urban areas are almost entirely excluded from the extent of *S. polita*, particularly San Juan and Caguas, which matches field observations. Additionally, *S. polita* appears to prefer higher elevations in wet conditions, with their range extending along the Cordillera Central, except for portions with the highest elevations, and into the Northern Karst region (Fig. 1c). The scattered patterns across the Northern Karst region are likely a product of the microclimate conditions from the abrupt elevation changes of the mogotes (limestone haystack hills). Similar to *A. graminifolia*, jackknife tests for *S. polita* reveal temperature variables are most important in determining *S. polita* presence, particularly the maximum temperature of the warmest month (Fig. S2c). Response curves for *S. polita* indicate an affinity for colder temperatures (Fig. S5), but with a higher tolerance for warmer temperatures than *A. graminifolia* (Fig. S3). This pattern results in *S. polita* absence at the lowest elevations (Fig. S5g). Additionally, the model suggests *S. polita* prefers consistent precipitation year-round, preventing presence in the seasonally dry forests along the southern coast of the island (Fig. S5d,f).

Co-occurrence maps reveal how variations and similarities in response to the selected environmental variables influence the degree of interspecific interactions. The distribution of *S. polita* excludes areas of high anthropogenic disturbance, providing a refuge for *D. crumenatum* in urban environments. (Figs. 2f and 3f). Even beyond urban areas, differences in the climate niches of both species likely leads to sparse overlap between the two populations across the island, with *S. polita* present in less than a third of *D. crumenatum*'s range (Table 1). In comparison, the similar response of *A. graminifolia* and *S. polita* to environmental variables results in significant overlap in their potential distributions (Figs. 2a and 3a). Higher tolerance for lower temperatures allows *A. graminifolia* to extend beyond *S. polita* at higher elevations in the western end of the Cordillera Central. Conversely, tolerance for higher temperatures by *S. polita* allows it to extend to lower elevations than *A. graminifolia* (Figs. 2a and 3a).

Table 1

Summary of percent change (from present) in size of modelled ranges for *Arundina graminifolia* (AG), *Dendrobium crumenatum* (DC) and *Stethobaris polita* (SP) and the percent of orchid range overlapping with *S. polita* across all modelled climate scenarios for years 2050 and 2070.

| Variable  | Present | CNRM2050<br>RCP2.6 <sup>a</sup> | CNRM2050<br>RCP8.5 | CNRM2070<br>RCP2.6 | CNRM2070<br>RCP8.5 | CCSM2050<br>RCP2.6 <sup>b</sup> | CCSM2050<br>RCP8.5 | CCSM2070<br>RCP2.6 | CCSM2070<br>RCP8.5 |
|---|---------|---------------------------------|--------------------|--------------------|--------------------|---------------------------------|--------------------|--------------------|--------------------|
| % change in AG range  | N/A     | -30.13                          | -57.33             | -55.52             | -85.14             | 2.24                            | -36.14             | -17.88             | -74.28             |
| % change in DC range  | N/A     | -23.53                          | -32.87             | -37.54             | -42.55             | -8.94                           | -15.73             | -12.82             | -29.74             |
| % change in SP range  | N/A     | -1.52                           | -21.82             | -32.69             | -59.51             | -1.24                           | -15.46             | -1.72              | -73.15             |
| % of AG range overlap with SP   | 67.93   | 73.88                           | 70.82              | 55.96              | 64.37              | 73.46                           | 79.04              | 74.53              | 58.09              |
| % of DC range overlap with SP   | 28.61   | 41.68                           | 46.62              | 21.90              | 30.07              | 42.19                           | 46.35              | 40.69              | 17.55              |
| <sup>a</sup> CNRM = Centre National de Recherches Météorologiques-Coupled Model 5 |         |                                 |                    |                    |                    |                                 |                    |                    |                    |
| <sup>b</sup> CCSM = Community Climate System Model 4                              |         |                                 |                    |                    |                    |                                 |                    |                    |                    |

#### Future species distributions and interactions based on climatic change models

As climate changes over the coming decades, so does the potential distribution of these three species. While there is variability among models, all except one predict a decrease in suitable habitat for each species, regardless of GCM, RCP or time period (Table 1). Under the CNRM model, there is a consistent trend of increasing losses for each species from rcp2.6 (2050) to rcp8.5 (2070), with rcp8.5 (2050) and rcp2.6 (2070) projecting similar range sizes (Fig. 4). This trend is not as clear in the CCSM model, which projects minimal losses in suitable habitat size for each species, except in rcp8.5 during 2070 (Fig. S6). Overall, the CCSM model has more conservative projections of suitable habitat loss than the CNRM model (Table 1).

Binary maps of these models reveal consistent projections of suitable habitat for the two GCMs. All models predict range shifts for *A. graminifolia* and *S. polita* to the center of the island, north of their current ranges in the Cordillera Central, with decreased suitability along the Cordillera Central and range retraction for *A. graminifolia* in El Yunque (Figs. 2b-e and 3b-e). Similarly, all models predict continued *D. crumenatum* presence in the San Juan-Caguas corridor, with some range expansion through the center of the island and some range retraction at certain lower elevations (Figs. 2g-j and 3 g-j). The main difference between GCMs is the size of suitable habitat within these regions.

Elevation histograms at predicted *D. crumenatum* suitable habitat do not suggest an altitudinal range shift under future climate scenarios, with many climate scenarios predicting a slight decrease in average elevation, rather than an increase (Figs. 5 and S7). This might be due to the model's prediction of continued *D. crumenatum* presence near sea-level San Juan (Figs. 2g-j and 3 g-j).

Generally, *S. polita* has lower projected losses in suitable habitat than either orchid (Table 1). Furthermore, declines in orchid suitable habitat do not result in proportional declines in their interaction with *S. polita*, suggesting both orchids may primarily lose suitable habitat that provide refuge from *S. polita* attack (Fig. 4), and/or that climate change creates new areas of overlap through range shifts (Figs. 2 and 3). As a result, a similar to greater proportion of the ranges of both orchids will be subject to enemy attack under models of climate change (Table 1). Climate change will only create orchid refuge from weevil attack (proportionally) in climate scenarios that predict substantial *S. polita* habitat reduction (Fig. 4b,d).

## Discussion

## Overview

Global invasions are on the rise and are doing so under an increasingly changing climate. To properly deal with these invasions, it is important to understand their potential scale across time and space. Similarly, it is important to identify biotic interactions and environmental variables that influence the establishment and spread of these invasions. If there is biotic resistance to non-native spread, determining the spatial heterogeneity of this interaction can provide insight into the propagule pressure driving the invasion. However, climate change over the coming decades –and beyond– is expected to alter species distributions and demography; potentially altering the spatial scale of invasions and their biotic interactions in the near future. Unfortunately, little to no previous research on how climate change will alter the distribution of invasions and the scale of biotic resistance. By studying the current and potential ranges of two naturalized orchids *Dendrobium crumenatum* and *Arundina graminifolia*, along with their acquired florivore and seed predator, *Stethobaris polita*, we have successfully modelled how climate change may influence the distribution of the two invaders and the spatial extent of their negative interactions with the weevil which may ultimately affect rate of spread or range contraction.

### Factors driving present distributions and biotic interactions

Land cover is the factor that is most associated with the distribution of *D. crumenatum* across Puerto Rico, with an overwhelming prevalence of naturalized *D. crumenatum* within urban areas. This abundance in urban centers is likely tied to their spread through the formal and informal horticultural trade, similar to many other ornamental plants (Mack and Erneberg 2002; Mack 2003). The more popular a plant is, the greater the propagule pressure and the higher the probability of invasional success (Dehnen-Schutz et al. 2007). The rapid spread of *Dendrobium crumenatum* across the island over the past decade is certainly connected to its increasing popularity among orchidists and other plant enthusiasts.

Rapid establishment and spread of *D. crumenatum* requires two critical processes: exploitation of mycorrhizal fungi and pollinator services. The orchid mycorrhizal fungi are parasitized at the seed germination stage as orchid seeds lack endosperm making them dependent on their fungi for nutrition, at least until the plants become fully photosynthetic (Bayman et al. 2002; Bellgard and Williams 2011; Meng et al. 2019). We do not know what fungi are involved, but one study in its native range identified *Epulorhiza* (Tulasnellaceae) as a fungal associate of *D. crumenatum* (Ma et al. 2003). Regardless, we expect that either the fungus is widespread in the tropics or the orchid has the capacity to exploit a wide range of fungal taxa. On the other hand, pollinator services are clear. *Dendrobium crumenatum* in its native habitat is pollinated by *Apis cerana* and *A. dorsata* (Hymenoptera: Apidae) (Brooks and Hewitt 1909; Leong and Wee 2013), but throughout much of its invaded range (including Puerto Rico), the orchid is pollinated by the perfect surrogate, *Apis mellifera*, which has been introduced worldwide. In Puerto Rico, *A. mellifera* occurs throughout the island, so pollinator services are not likely limiting anywhere on the island (Ackerman 2017; Ackerman in press).

Since *D. crumenatum* is a recent invasion, the evidence of recruitment from initial cultivation is profound. Almost all naturalized populations of *D. crumenatum* appeared to be sourced from nearby cultivated parent plants. Many orchids were planted in front yards along roadsides, and the role of roads as an effective corridor for non-native seed dispersal has already been identified (Parendes and Jones 2000; Mortensen et al. 2009). Rivers are also likely corridors for *D. crumenatum* spread because windflow vectors the ultralight seeds and the higher humidity promotes seedling establishment of epiphytic orchids (e.g., Scheffknecht et al. 2010; Olaya-Arenas et al. 2011; Crain 2012). Currently, we are aware of only two populations along riparian habitats, but as the orchid continues to spread over the coming decades, we can expect more riverine populations without an identifiable source population, similar to what we currently observe with most *A. graminifolia* populations.

Land cover provides widespread refugia for *D. crumenatum* from *S. polita* attack, adding another complementary aspect in facilitating *D. crumenatum* establishment within those areas. An increase in abundance of non-native species with a concurrent decrease in native species towards urban centers is a widely observed phenomenon (Almasi 2000; McKinney 2002; Burton et al. 2005). Our findings reaffirm the absence of *S. polita* in the urban matrix (Soifer and Ackerman 2019). With a majority of *D. crumenatum* residing almost entirely within urban and suburban areas, there is little co-occurrence with *S. polita* and limited biotic interaction (Fig. 5).

However, the modelled proliferation of *D. crumenatum* primarily within urban centers might also be due to spatial sampling bias, with most populations found within the San Juan-Caguas corridor overemphasizing the role that land use has in determining *D. crumenatum* establishment. Conversely, it might be underpredicting suitability within natural areas where *S. polita* is abundant. It may be just a matter of time for *D. crumenatum* to become a common fixture in forested areas. After all, it has only been noticeably naturalized for less than two decades.

The two processes for successful establishment and spread of *A. graminifolia* are similar as that of *D. crumenatum*: exploitation of mycorrhizal fungi and pollinator services. The fungus associated with *A. graminifolia* is a *Tulasnella* species retrieved from seedlings in a population in Yunnan Province, China (Meng et al. 2019). We do not know whether this is a widespread fungus, or that *A. graminifolia* exploits

other fungi in its extensive native and non-native range. However, pollinator services are clear. Flowers are self-compatible but not self-pollinating (Huda and Wilcock 2012). Unlike the nectar producing *D. crumentatum*, *A. graminifolia* attracts pollinators by deceit, offering no reward to foraging pollinators. In its native range, *A. graminifolia* is pollinated by multiple species, and is a pollinator generalist (Sugiura, 2014). In Puerto Rico, *A. graminifolia* is pollinated by *Apis mellifera*, but also by *Centris haemorrhoidalis*, a larger solitary bee. Both occur throughout the current range of *A. graminifolia* on the island (Ackerman 2017; Ackerman in press).

While *A. graminifolia* is a popular ornamental plant in Puerto Rico, its proliferation along remote roadsides within mountain forests coincides with localities in its native habitat (Dressler 1981; Chen et al. 2009).

Major urban centers that provide orchids refuge from *S. polita* attack are all found at lower elevations in Puerto Rico, and do not overlap with the distribution of the mid to high-elevation *A. graminifolia*. As a result, land cover does not provide refuge for *A. graminifolia* from *S. polita* attack, except perhaps in the western end of the Cordillera Central (Fig. 2a). This region appears to have climate barriers to *S. polita* survival (Fig. S3), but it accounts for only about a third of *A. graminifolia*'s current potential range.

The present degree of overlap between both orchids and the weevil suggest interactions with *S. polita* are not preventing non-native orchid establishment. Indeed, prolific populations of *A. graminifolia* exhibited weevil damage. Nonetheless there is likely some degree of biotic resistance as was shown for another invasive orchid in Puerto Rico, *Spathoglottis plicata*, which had positive growth rates despite heavy infestations of *S. polita*. Demographically, the weevils extended lag times thereby slowing orchid population growth and just delaying the inevitable (Falcón et al. 2017). Future research is needed to investigate the specific demographic effects of *S. polita* attack on *A. graminifolia* and *D. crumentatum*, and how they might compare to the previously studied effects on invasive and native orchids (Recart et al. 2013).

#### Distributions and biotic resistance under climate change

While climate change is largely expected to facilitate global invasions, our study shows climate change decreasing the size of suitable habitat for two non-native orchids in Puerto Rico. Despite each orchid occupying contrasting climate niches, both species are expected to experience similar trends in range contraction due to climate change (Table 1). Climate responses are regionally-specific, but invasive range-reduction under climate change has been predicted in other studies (Beaumont et al. 2009; Bradley et al. 2009; Kolanowska and Konowalik 2014). While higher CO<sub>2</sub> levels and increased global commerce should continue to promote plant invasions in the future, climate changes may promote some invasions while restricting others (Bradley et al. 2010).

Multiple studies have illustrated how climate change can invoke independent responses among interacting species, creating novel communities and altering existing ones (Schweiger et al. 2008; Van der Putten et al. 2010; Stewart et al. 2015). In this case, our models generally suggest future climate change will increase the proportionate interaction between the non-native orchids and the weevil, with interaction levels remaining the same or decreasing only in climate models predicting massive range reduction for *S. polita* (Table 1). This is a result of two phenomena: areas where orchid populations are currently free from weevil attack are no longer suitable under models of climate change, and/or climate change is expected to create range shifts that increase the overlap between *S. polita* and either orchid. Indeed, our models predict *S. polita* will largely interact with both orchids in areas where they are not currently interacting (Figs. 2 and 3). Additionally, projected increases in the interaction may be attributed to higher resilience to expected climate change for the weevils than either of the two non-native orchids (Fig. 4). Response curves reveal *S. polita* has a more generalized niche than either of the orchids, which can be expressed in its interactions with two orchids in opposing climate envelopes (Fig. S3-5). While having a broader niche than host plants is expected for polyphagous insects (Stewart et al. 2015), *S. polita* is an orchid specialist. Nonetheless, we anticipated that the weevil would have niche flexibility since the orchid family is species-rich, the weevil exploits species in all three subfamilies present within its range, and its native orchid hosts often occur in small, hyperdispersed populations (Stewart et al. 2015; Brewster and Ackerman 2013; Tremblay and McCarthy 2014).

The future distribution of the three focal species can have important implications for the surrounding community. The invasion of non-native orchids in Puerto Rico has been a demographic boom for *S. polita* by providing abundant resources throughout the year. Unfortunately, this can have spillover effects on native orchids increasing the frequency of attack and reducing their reproductive output (Recart et al. 2013). The outlook does not look promising unless climate-driven range shifts are non-parallel among interacting species, which is not the case for either *A. graminifolia* or *D. crumentatum*. Except for a few species, we currently do not have sufficient data to assess the current and future distributions of the orchid flora.

When interpreting climate change SDMs, it is important to recognize that models work to show what is possible. Projected range shifts will not necessarily occur because dispersal capabilities and conditions for germination and establishment will determine if and where species move within climatically suitable areas. In some cases, dispersal limitations can impede invasions more than biotic resistance (Moser et al. 2011). Schweiger et al. (2008) found that the dispersal capabilities of interacting species are highly influential in determining their future

distributions, with significant expansions in distribution with unlimited dispersal (goes everywhere that is predicted suitable), but significant decreases when dispersal is highly restricted (future range only includes overlap between present suitability and future suitability). While true unlimited dispersal is ecologically unrealistic, the continued spread of *A. graminifolia* and *D. crumenatum* in the horticultural trade and their production of many thousands of wind-dispersed seeds within a single fruit should not make either orchid dispersal-limited. All orchids require mycorrhizal fungi for successful germination, but the apparent ease at which the two orchids spread suggests that their distributions may not be limited by the lack of appropriate fungi, at least not beyond the microsite scale. As for *S. polita*, it does oviposit within orchid fruits, tying its own dispersal to that of its host plants, but the weevil is not dependent on just one host species. Since suitable range sizes are projected to decrease for all three species under climate change, any dispersal limitations that prevent modelled range shifts would make the range reductions of the three species greater than what our model predicts.

One important consideration to make in interpreting our results is the ever-changing nature of land use. Since we cannot accurately predict landscape or land use changes in the coming decades, land cover was held constant across all climate projections. However, it is expected for land use to change in the future through either human actions (Martinuzzi et al. 2007), climate change (Khalyani et al. 2016), or natural succession (Chinea, 2002). As urban areas move and change, so might the scale of the interaction between *S. polita* and *D. crumenatum*.

Contrary to our predictions, our models showed no evidence of an altitudinal range shift for *D. crumenatum* under projected climate change. In fact, the distribution of projected *D. crumenatum* populations along the elevation gradient remains consistent from the present day through various projected climate scenarios. With land use being held constant through future climate scenarios, their continued presence in those areas despite an altered climate might be due to tolerance for heat as long as there is sufficient precipitation, or a spatial sampling bias towards urban centers like San Juan, which are at sea level. Even if our sampling was biased, we have no evidence of an altitudinal range shift towards mid to higher elevations (Fig. 5).

Species distribution models can provide important insight into the future distributions of invasions and of their acquired interactions; however, they provide an incomplete picture of novel community structure and population dynamics within suitable regions. The next step in understanding the future of *A. graminifolia*, *D. crumenatum* and other orchid invasions on Puerto Rico is assessing how climate change will influence their interactions with pollinators, ants, herbivores, seed predators, and mycorrhizal fungi; especially since there is growing literature on climate-induced phenological uncoupling between interacting species (Thackeray et al. 2010; Walther 2010). Finally, future research should monitor the effects that *A. graminifolia* and *D. crumenatum* have on native orchids through apparent competition (Recart et al. 2013).

Considering the positive attitudes towards invasive orchids, their mitigation and eradication is likely unpopular and possibly not economically worthwhile (Ackerman 2007). Although the overall ecological effects of climate change are expected to be overwhelmingly negative, it can directly and indirectly mitigate invasions where human intervention will likely not occur. While climate change will not eliminate either orchid from Puerto Rico in the next 50 years, our analyses indicate that it might do so if climate trends continue in the next century.

Climate change can have a profound effect on species distributions and interactions, and these effects have important implications within the context of invasions. Non-analogous responses to climate change between invaders and their acquired enemies can create or alter spatially-heterogeneous outcomes to such interactions. To the best of our knowledge, this study is one of the first to model the changing spatial relationships between plant invaders and an acquired enemy that may offer some measure of biotic resistance now and in the future.

## Declarations

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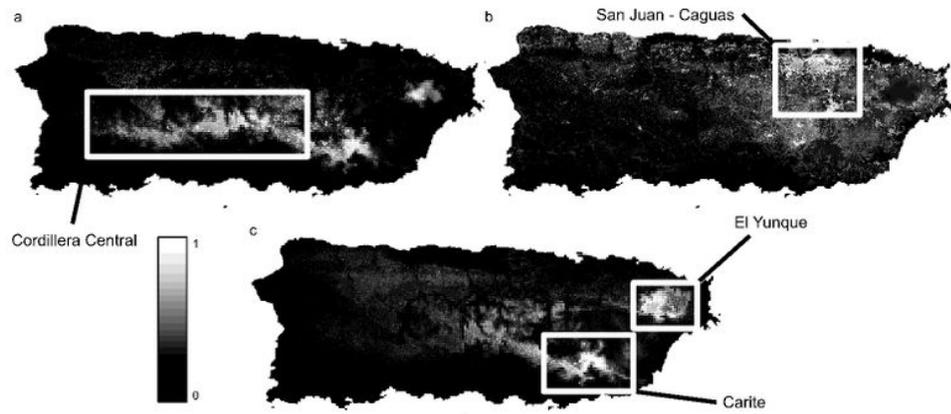
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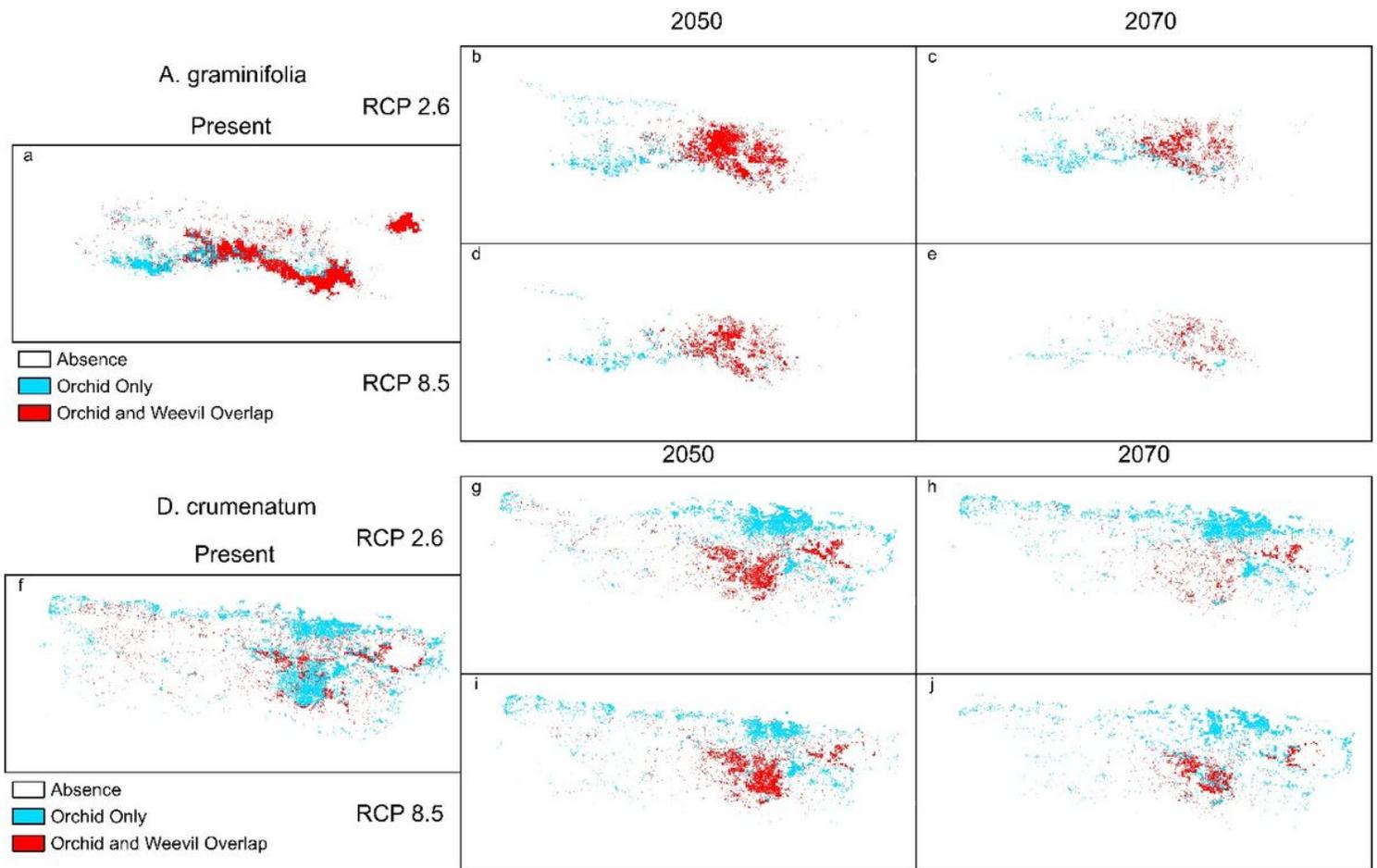
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## Figures



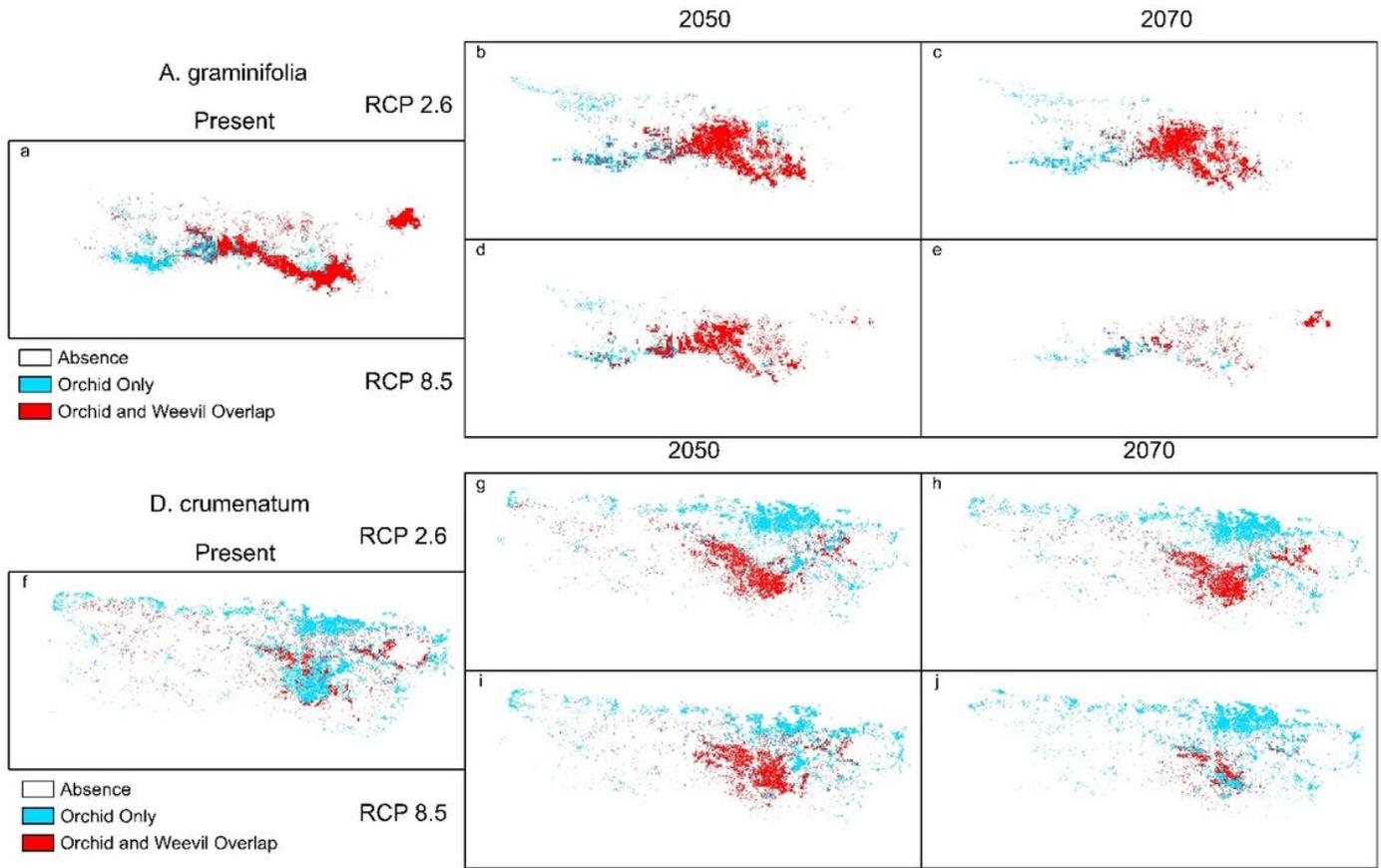
**Figure 1**

Average distribution models in the present day for *Arundina graminifolia*, *Dendrobium crumenatum* and *Stethobaris polita*. Lighter colors indicate higher probability of presence. Models produced using 10-fold cross validation. a Probability of presence for *A. graminifolia* (AUC =  $0.922 \pm 0.076$ ). b Probability of presence for *D. crumenatum* (AUC =  $0.915 \pm 0.031$ ). c Probability of presence for *S. polita* (AUC =  $0.885 \pm 0.061$ ). Boxes identify notable regions on the island



**Figure 2**

Binary maps of *Arundina graminifolia* (a-e) and *Dendrobium crumenatum* (f-j) suitable habitat above threshold (*A. graminifolia* = 0.2458; *D. crumenatum* = 0.3345; *Stethobaris polita* = 0.1834) and where they overlap with *S. polita* in the present, and in two Representative Concentration Pathways during 2050 and 2070 (CNRM)



**Figure 3**

Binary maps of *Arundina graminifolia* (a-e) and *Dendrobium crumenatum* (f-j) suitable habitat above threshold (*A. graminifolia* = 0.2458; *D. crumenatum* = 0.3345; *Stethobaris polita* = 0.1834) and where they overlap with *S. polita* in the present, and in two Representative Concentration Pathways during 2050 and 2070 (CCSM)

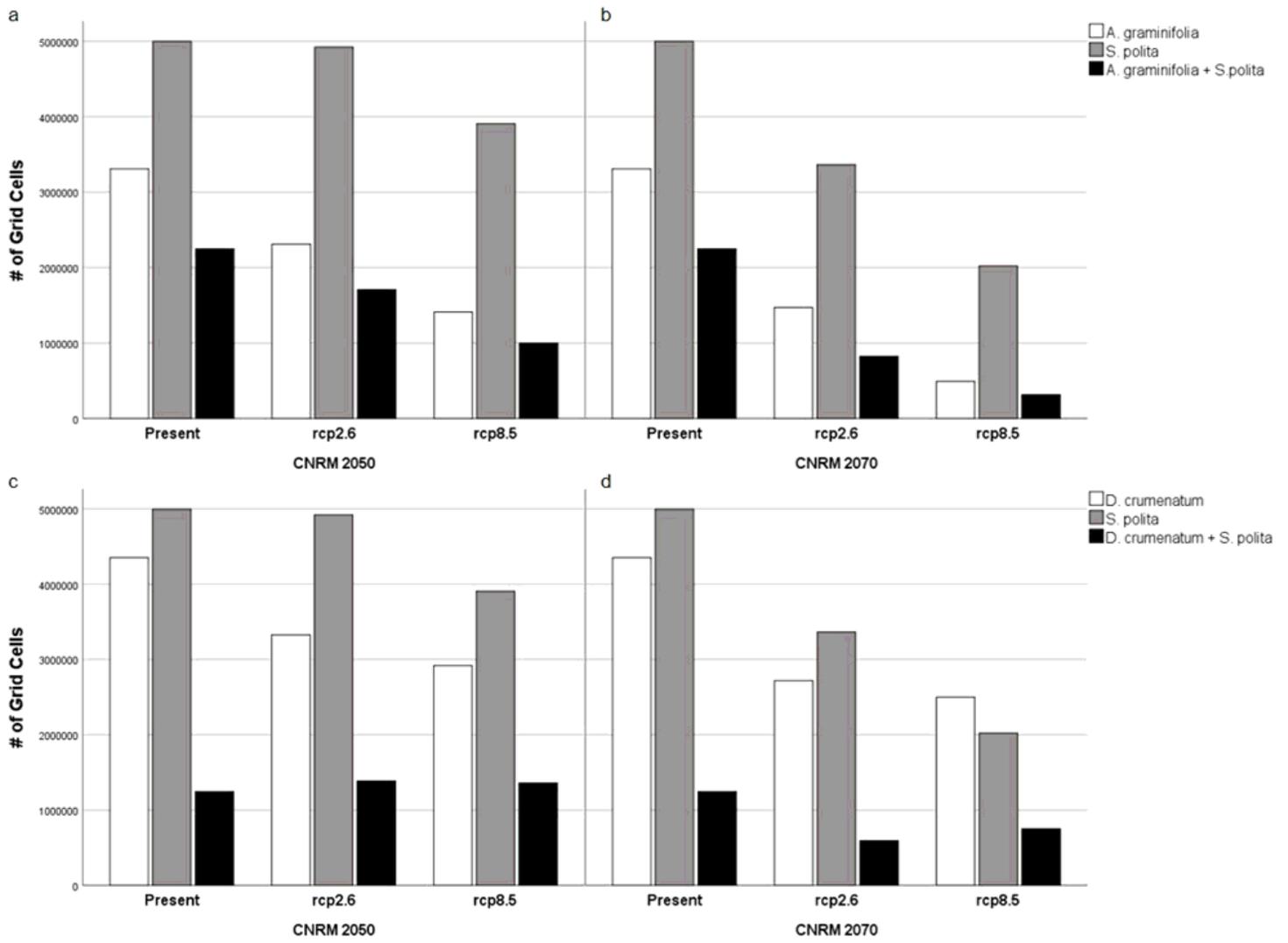
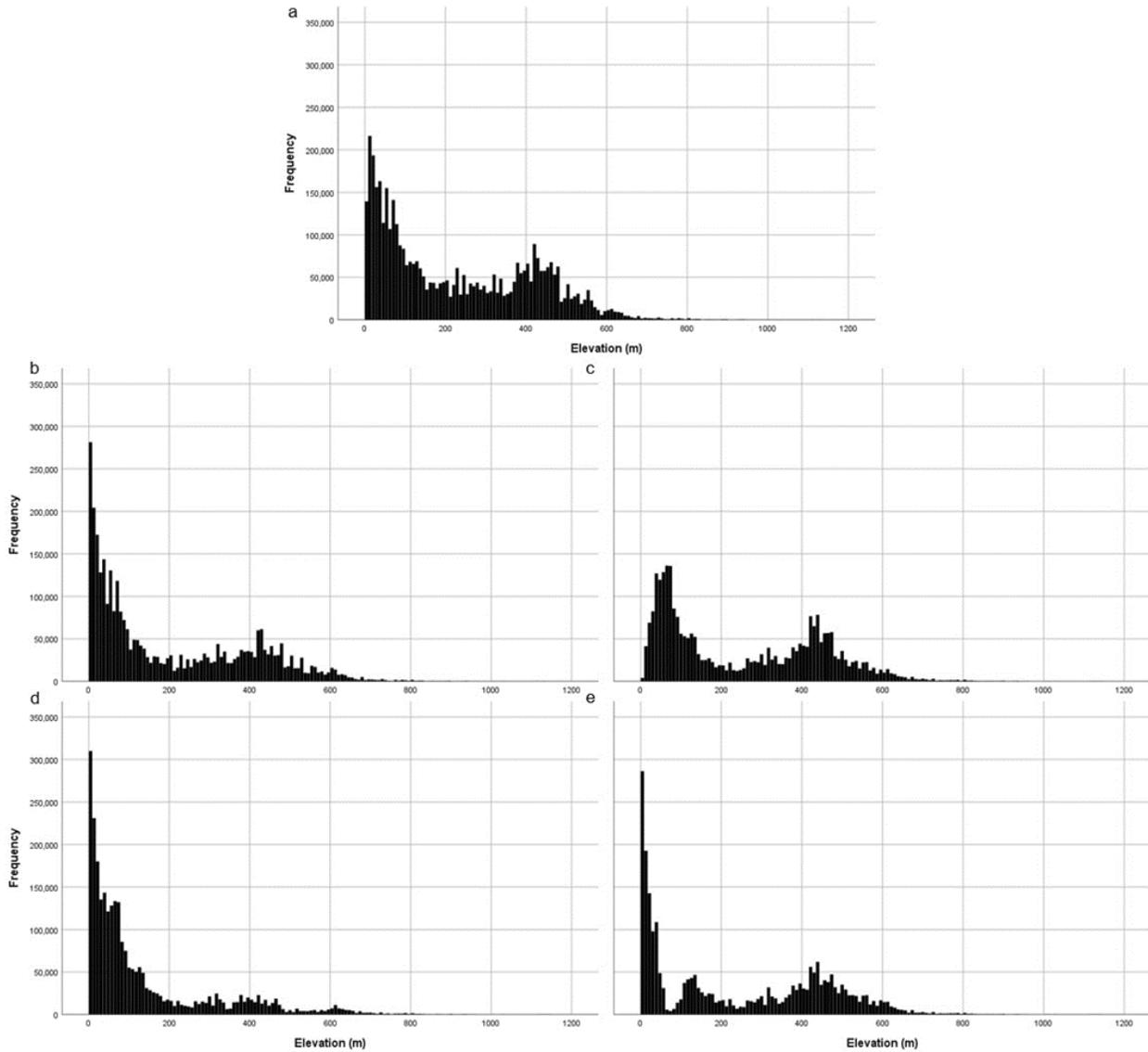


Figure 4

Number of occupied grid cells above the threshold for *Stethobaris polita* with *Arundina graminifolia* (a-b) and *Dendrobium crumenatum* (c-d) for present day and two Representative Concentration Pathways in 2050 (a, c) and 2070 (b, d) under the CNRM model



**Figure 5**

Elevation values at *Dendrobium crumenatum* presence cells in the present (a), 2050 (b-c) and 2070 (d-e) in RCP 2.6 (b,d) and rcp 8.5 (c, e) from the CNRM model. a Elevations in present day ( $x = 225.68 \pm 186.119$ ). b Elevations in 2050 under rcp 2.6 ( $x = 202.78 \pm 193.094$ ). c Elevations in 2050 under rcp 8.5 ( $x = 254.95 \pm 193.583$ ). d Elevations in 2070 under rcp 2.6 ( $x = 135.99 \pm 165.23$ ). e Elevations in 2070 under rcp 8.5 ( $x = 241.43 \pm 213.224$ )

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [OrchidInvasionsSupplementaryMaterial.docx](#)