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Terrestrial orchids in a tropical forest: best sites for abundance differ from those for reproduction

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Abstract. Suitable habitat for a species is often modeled by linking its distribution patterns with landscape characteristics. However, modeling the relationship between fitness and landscape characteristics is less common. In this study we take a novel approach towards species distribution modeling (SDM) by investigating factors important not only for species occurrence, but also abundance and physical size, as well as fitness measures. We used the Neotropical terrestrial orchid *Prescottia stachyodes* as our focal species, and compiled geospatial information on habitat and neighboring plants for use in a two-part conditional SDM that accounted for zero inflation and reduced spatial autocorrelation bias. First, we modeled orchid occurrence, and then within suitable sites we contrasted habitat characteristics important for orchid abundance as compared to plant size. We then tested possible fitness implications, informed by analyses of allometric scaling of reproductive effort and lamina area, as well as size–density relationships in areas of *P. stachyodes* co-occurrence. We determined that orchid presence was based on a combination of biotic and abiotic factors (indicator species, diffuse solar radiation). Within these sites, *P. stachyodes* abundance was higher on flat terrain, with fine, moderately well-drained soil, and areas without other native orchids, whereas plant size was greater in less rocky areas. In turn, plant size determined reproductive effort, with floral display height proportionate to lamina area (more photosynthates); however, allometric scaling of flower quantity suggests a higher energy cost for production, or maintenance, of flowers. Overall, habitat factors most important for abundance differed from those for size (and thus reproductive effort), suggesting that sites optimal for either recruitment or survival may not be the primary source of seeds. For plots with multiple *P. stachyodes* plants, size–density relationships differed depending on the size class examined, which may reflect context-dependent population dynamics. Thus, ecological resolution provided by SDM can be enhanced by incorporating abundance and fitness measures.

Key words: local distribution; Luquillo Forest, Puerto Rico; Orchidaceae; *Prescottia stachyodes*; reproductive effort; size–density; source–sink; species distribution modeling; tropical wet forest; two-part conditional model; vegetative trait allometry; zero inflation.

INTRODUCTION

A central goal in ecology is to understand the underlying mechanisms that determine where a species is found (Brown et al. 1995, Brotons et al. 2004, Cunningham and Lindenmayer 2005, McCormick and Jacquemyn 2014) and how this relates to fitness (Mróz and Kosiba 2011, Lasky et al. 2014). Species distribution modeling (SDM) can provide valuable insights on the environmental characteristics underlying where a species is located (Franklin 2009, Peterson et al. 2011). These models are important for conservation of rare species (Brown et al. 1995, Cunningham and Lindenmayer 2005, Potts and Elith 2006), control of invasive species

(Latimer et al. 2009), or estimates of ecosystem recovery after disturbance (Thompson et al. 2002, Comita et al. 2009, Lasky et al. 2014). One shortcoming of SDMs is that they rarely incorporate metrics of fitness or test principles of ecological theory; however, there is growing incentive to develop more mechanistic SDMs that incorporate eco-physiological knowledge (Kearney and Porter 2009, Douma et al. 2012), population dynamics or biotic interactions (Guisan and Thuiller 2005), or trait-mediated patterns of survival (Lasky et al. 2014).

In the *sensu stricto* definition of the term, SDMs are based on both species presence and absence (Brotons et al. 2004, Peterson et al. 2011), with relaxed interpretation using presence-only data. Other metrics, such as abundance (i.e., count data or density), can also be incorporated. However, relying on abundance data exclusively can be misleading, especially if high values are indicative of dispersal limitation rather than habitat

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optimum (Condit et al. 2000). Using a combination of both presence–absence and abundance data within SDMs can help to distinguish between sites suitable not only for colonization, but also for recruitment or survival (Brown et al. 1995). Identifying factors that influence population distributions or establishment is an important, yet challenging, goal for organisms with complex ecological relationships that change depending on life history stage (Tremblay et al. 2006, Comita et al. 2009, McCormick and Jacquemyn 2014).

Further issues with SDMs include fitting zero-inflated data sets, with an excess of zeros compared to a Poisson distribution (Barry and Welsh 2002, Cunningham and Lindenmayer 2005, Martin et al. 2005, Potts and Elith 2006). Zero inflation can arise for a variety of reasons, with “true zeros” attributed to ecological processes that contribute to species rarity or absence from otherwise suitable habitat, rather than sampling error (Martin et al. 2005). Fortunately, there are a variety of modeling options that are appropriate for instances of zero inflation, either using a specialized single-model format (e.g., mixed models, Bayesian hierarchical models), or using a “hurdle model” (Cragg 1971), which is a two-stage process based on first modeling species presence, then abundance conditional upon species presence. This two-part approach generally performs better than other modeling techniques (i.e., Poisson, negative binomial, quasi-Poisson) as noted by Potts and Elith (2006), and aids the ecological understanding of rare species (Cunningham and Lindenmayer 2005). The two-part approach can also incorporate generalized additive model (GAM) methods for added flexibility (Barry and Welsh 2002) and smoothing components to reduce spatial autocorrelation of the residuals (Dormann et al. 2007).

A different approach toward identifying suitable habitat is to examine the connection between plant traits and abundance (Cornwell and Ackerly 2010), and how these values change along environmental gradients (Mróz and Kosiba 2011, Douma et al. 2012). For instance, plant size is determined by whatever resource (e.g., light, moisture, nutrients) is crucial, yet most limited (von Liebig 1847). This resource limitation can create an allocation trade-off, with responses that vary depending on age or life history strategy (Otero et al. 2007). Energy may be used toward acquisition of more resources (e.g., leaves above ground, roots below), maintenance of preexisting structures, or the cost of reproduction or defense (Chapin et al. 1985, Müller et al. 2000). Plants at sites with greater resource availability are therefore expected to have less severe trade-offs and thus increased chances of survival.

Beyond identifying suitable environmental conditions, there is also a need to link location with possible fitness differences. To do this, one may test the allometric relationships between vegetative and reproductive structures (Mróz and Kosiba 2011), and then make informed inferences about fecundity (Aarssen and Taylor 1992).

For instance, larger plants with more leaf surface area have a greater photosynthetic potential than smaller plants, and are likely to have more resources to allocate toward reproduction (Chapin et al. 1985).

We performed a SDM for the terrestrial orchid *Prescottia stachyodes* (Sw.) Lindl., but added a novel series of steps to also examine fitness measures. To do this, we used a two-part conditional modeling approach suitable for zero-inflated data (Cragg 1971, Barry and Welsh 2002, Cunningham and Lindenmayer 2005), while also reducing spatial autocorrelation in the residuals (Dormann et al. 2007), and then linked these results with reproductive effort and size–density relationships. First, we modeled orchid distribution using presence–absence data. Then, within suitable habitat where orchids were present, we modeled orchid abundance as well as plant size. Next, we tested allometric relationships between reproductive effort and lamina area. Lastly, we examined patterns of co-occurrence, specifically whether plant size is a function of density. A diagram of our SDM process is illustrated in Fig. 1 and Appendix A: Fig. A1.

A priori, we predicted orchid occurrence to be highest in areas with less historic land use disturbance. Orchid abundance was thought to be indicative of seed germination or seedling survival; thus, we expected optimum habitat to have flat, moist terrain (avoiding washout, yet providing water for protocorms), and presence of positive indicator species (Dufrene and Legendre 1997, McCune and Mefford 1997). Larger plants were expected on hilltops or slopes with higher solar radiation, and in less rocky areas. Lamina area was expected to determine reproductive effort (based on energy available from photosynthesis), with isometric scaling. A negative size–density relationship was expected for co-occurring orchids, similar to observations of other herbaceous monocots (Weller 1987).

MATERIALS AND METHODS

Species and study site

We chose the terrestrial orchid *Prescottia stachyodes* as our model species because it is common and non-weedy; co-occurring with both rare (Bergman et al. 2006) and invasive orchids (Cohen and Ackerman 2009). The range of *P. stachyodes* includes forest habitats from mid-to-high elevations in Brazil, Venezuela, Colombia, Central America, Mexico, and throughout the West Indies (Ackerman 1995, 2014). *Prescottia stachyodes* has persistent foliage, shallow, fleshy roots, and several dark green elliptical leaves (Ackerman 1995). From February to March, *P. stachyodes* produces a slender and erect raceme covered with dozens of small green flowers that are either self-pollinating or visited by moths (Ackerman 1995, Singer and Sazima 2001). *Prescottia stachyodes* has high fruit set, ranging from 52% to 98%, and produces thousands of small, dust-like, wind-dispersed seeds (Ackerman 1995, Singer and Sazima 2001). To germinate, orchids rely on external nutrients acquired

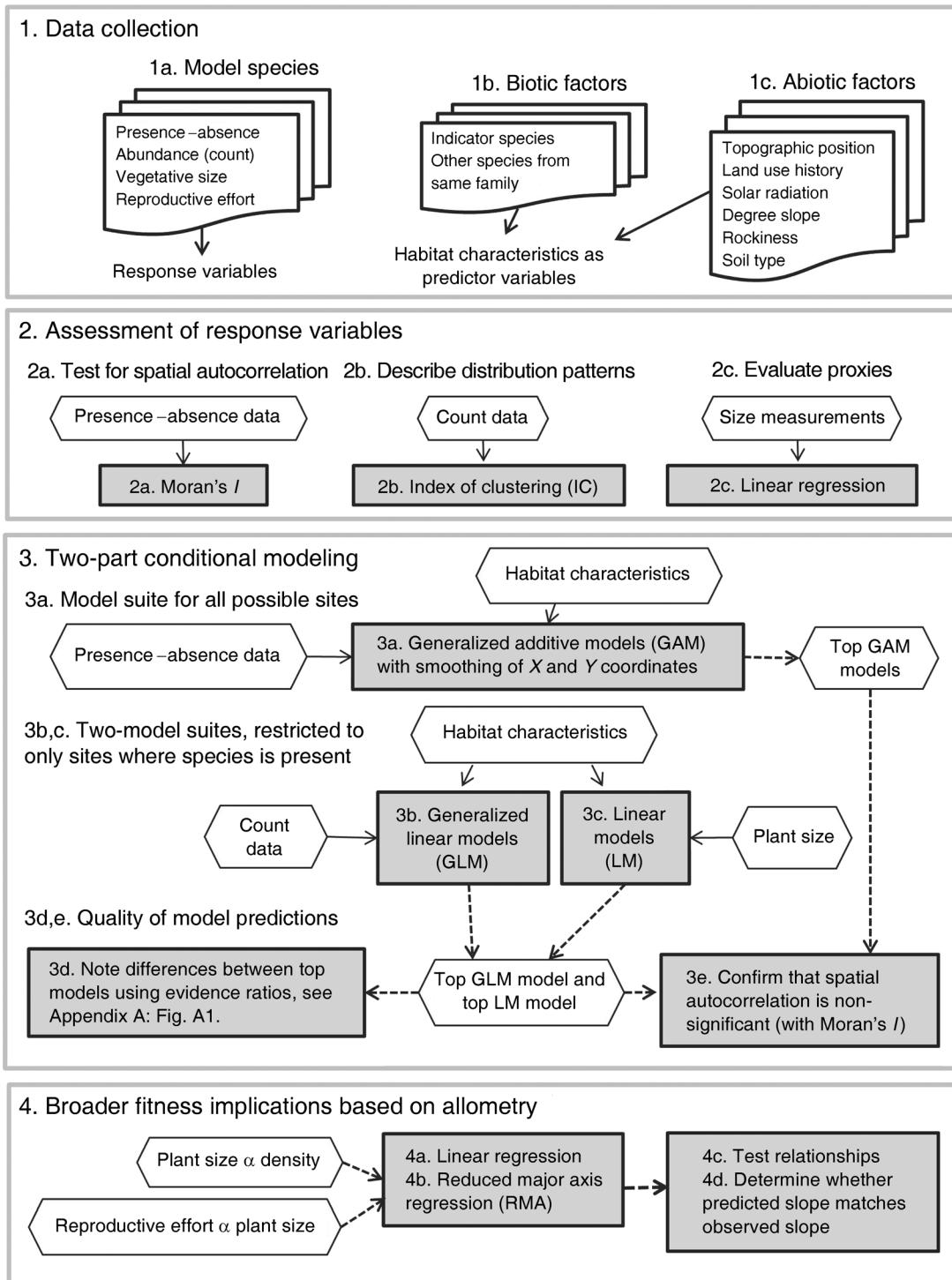


FIG. 1. Diagram of the species distribution modeling (SDM) process for a two-part conditional model suitable for zero-inflated data, with novel incorporation of both abundance and plant size as indicator of fitness. Overall methods include: (1) data collection; (2) assessment of response variable; (3) two-part conditional model starting with a generalized additive model (GAM) of species presence-absence, including steps to reduce bias of spatial autocorrelation (smoothing for *X*, *Y* coordinates), followed by a generalized linear model (GLM) for abundance and a linear model (LM) for plant size, with additional steps to assess model quality; and (4) assessment of fitness measures and testing allometric scaling predictions. Top models were selected using Akaike's information criterion (AIC) and/or Bayesian information criterion (BIC). The overall goal of this SDM process was to understand not only suitable habitat for species of interest, but also broader fitness implications.

from mycorrhizal fungi (e.g., Jacquemyn et al. 2007, Jersáková and Malinová 2007, Gowland et al. 2011, Bunch et al. 2013, McCormick and Jacquemyn 2014). Although mycorrhizal surveys have been made of tropical epiphytic orchids, at present little is known of the orchid–fungal relationships among tropical terrestrial species, including *P. stachyodes* (Otero et al. 2002).

Our study site was the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid near the El Verde Field Station, Puerto Rico (18°18' N, 65°47' W), in forest dominated by tabonuco trees (*Dacryodes excelsa* Vahl) at 350–500 m in elevation. The study area is within the subtropical wet forest zone (Holdridge Life Zone system; Ewel and Whitmore 1973) and has a minimum of 200 mm of rain per month (Brown et al. 1983). Habitat includes mostly primary forest (with some historical selective logging), and secondary forest that was once used for grazing, intensive logging, agriculture, and coffee plantations (Thompson et al. 2002). Since 1934, human disturbance has been drastically reduced and has been minimal for about seven decades; canopy coverage is now ~100% (Thompson et al. 2002).

Recording orchid distribution, abundance, and size

The LFDP grid is divided into 20 × 20 m plots, further subdivided into 5 × 5 m subplots. We used six 10 × 500 m transect lines containing 1200 subplots spanning areas with differing ecological characteristics as well as disturbance history. These subplots were identical to those used by prior orchid studies (Bergman et al. 2006, Cohen and Ackerman 2009), but with data collected independently from those projects.

We recorded *P. stachyodes* presence–absence, and abundance, per 5-m² subplot during the nonflowering season from June to August 2005; data were then used as response variables for modeling. All orchids with a minimum of one leaf were included, with sampling of plants at all life stages. Spatial patterns of *P. stachyodes* were described using Moran's *I* (Moran 1950) and the index of clumping (David and Moore 1954).

Because vegetative traits were highly correlated (\log_{10} -transformed lamina area, number of leaves, petiole length), we used lamina area as a proxy for overall plant size (Appendix B: Table B1). We estimated lamina area using the equation $((0.71 \times \text{width in cm} \times \text{length in cm}) - 0.97)$, based on photos of leaves ($n = 40$) measured using the program ImageJ (Abramoff et al. 2004). Measures of vegetative traits (proxy for plant size) from the largest orchid per subplot (expected to be mature and able to reproduce) were then used as a response variable for modeling size.

Associations with neighboring species

We anticipated that neighboring species would be important as a SDM factor because of the indirect ecological associations between orchids and neighboring plants, linked via shared facultative relationships with mycorrhizal fungi (Otero et al. 2002, Jersáková and

Malinová 2007, McCormick and Jacquemyn 2014). To identify significant positive or negative relationships between *P. stachyodes* and other species, we performed an indicator species analysis (Dufrene and Legendre 1997), using data on the relative abundance and frequency of 118 woody plant species, analyzed with the program PC-ORD version 4.0 (McCune and Mefford 1997). Our methods were identical to those used by Bergman et al. (2006) with the locally sympatric orchid *Wullschlaegelia calcarata* Benth. (an orchid associated with 32 indicator species), allowing us to make more direct comparisons between studies and to promote a deeper understanding of tropical orchid–tree relationships. Forest data came from the LFDP census (completed in 2002) of all species >1 cm diameter at breast height, archived by the Luquillo Experimental Forest-Long Term Ecological Research (LEF-LTER) program (*available online*).⁴ We also conducted separate indicator species analyses for subplots with differing disturbance history. Significance values were based on a Monte Carlo simulation, where orchid locations were randomly assigned 1000 times. Second, we categorized the co-occurrence of indicator species in four ways: (1) positive indicator species; (2) negative indicator species; (3) both positive and negative indicator species; or (4) no indicator species. This simplified indicator species metric was then used for modeling orchid occurrence, abundance, and size.

Habitat characteristics

Abiotic habitat characteristics per subplot were derived or interpolated from spatially explicit data using the geographic information system (GIS), ArcInfo version 9.3 (ESRI 2004). Geospatial data was provided by LEF-LTER (URL in footnote 4). Attribute values were based on where the centroid of each 5 × 5 m subplot intersected with a geospatial layer of interest. Geospatial layers for soil characteristics and rockiness were based on surveys conducted by the U.S. Department of Agriculture (Vick and Lynn 1995). To ensure sufficient sample size for modeling, we used the most common soil types (Zarzal and Cristal), and grouped rockiness into two categories: “less rocky” (very bouldery, extremely bouldery) and “more rocky” (rubbly, very rubbly). We created a topographic position layer (seat, slope, or top) based on transect notes by E. Bergman and C. Torres (*personal communication*). Historical land use classes were categorized by Thompson et al. (2002) based on aerial photographs from 1936; we grouped sites with <80% canopy cover as “more disturbed” and sites with >80% canopy cover as “less disturbed.” We created a digital elevation model (DEM) raster using ordinary kriging (spherical) of 442 ground-surveyed elevation points from the corners of each 20-m plot, extending beyond the LFDP grid to reduce edge

⁴ <http://luq.lternet.edu/data>

error. These DEM methods are similar to other Center for Tropical Forest Science (CTFS) plots (Condit 1998). Degree slope and diffuse solar radiation rasters were interpolated using ArcGIS Spatial Analyst Tools (ESRI 2004) and had 5-m spatial resolution that aligned with the LFDP subplots. Collinearity was noted between degree slope and diffuse solar radiation; however, these factors were hypothesized to be biologically important. Thus, to disentangle unique contributions per factor, we used the residuals from a linear regression of solar radiation as a function of degree slope (Graham 2003).

Species distribution models and model selection process

To address the zero inflation of our data set, we adopted a two-part conditional modeling process (Cragg 1971, Barry and Welsh 2002, Cunningham and Lindenmayer 2005, Potts and Elith 2006). First, we modeled orchid presence and absence across the 1200 LFDP subplots using a suite (set) of binomially distributed generalized additive models (GAM) with a logit link function suitable for zero-inflated data sets and with the ability to add, if needed, a smoothing function (for X , Y coordinates) to reduce (but not explicitly account for) spatial autocorrelation (Dormann et al. 2007). Other modeling methods can also be used for zero inflation or spatial autocorrelation, but most likely these methods would have produced only a subtle difference in results (Martin et al. 2005, Latimer et al. 2009). Next, within sites where *P. stachyodes* orchids were present, we used a suite of zero-truncated (positive-Poisson) generalized linear models (GLM) with a logistic link function for abundance. As a point of comparison, we also modeled plant size (normally distributed) using a suite of linear models (LM) with predictor variables identical to those of the GLM suite (Fig. 1; Appendix A: Fig. A1, Appendix C: Tables C2 and C3) and with data spatially joined by using the same LFDP subplots.

For each SDM suite (GAM, GLM, LM), we included (1) a null model; (2) simple models with one or two predictor variables; (3) more complex models based directly on hypotheses; and (4) a global model of all possible factors and interactions examined (Anderson and Burnham 2002). The GAM set included 45 models, and the GLM and LM set each contained 28 models. The “top model” selected per suite was based on a combination of the following: low Akaike’s information criterion (AIC; Akaike 1974) and Bayesian information criterion (BIC) scores, model weights (while also checking for possible over-fitting of data), and constancy of predictor variables included in highly ranked AIC and BIC models. When two models had similar delta values, we favored the one with the fewer parameters. To estimate GAM accuracy, we used receiver operating characteristics (ROC) area under the curve (AUC) values (Hanley and McNeil 1982). For model evaluation, we plotted model fit, checked model residuals for spatial autocorrelation using Moran’s I statistic, tested for correlation between observed and predicted values

using Spearman’s rank, and calculated root mean square error (RMSE) and average error (AVE_{err}), similar to Potts and Elith (2006). All models were run with R version 3.1 (R Development Core Team 2013), with the packages AICcmodavg, countreg, MASS, mgcv, ncf, spdep, stats (Venables and Ripley 2002, Wood 2011, Bjornstad 2013, Mazerolle 2013), and script (Dormann et al. 2007).

For the second step of the modeling process, it was noted that *P. stachyodes* abundance and plant size were correlated (Kendall rank correlation, $\tau = 0.22$, $P = 0.008$), a situation that we expected at the local scale (Cornwell and Ackerly 2010). To differentiate which habitat characteristics most strongly influence each response variable, we used a novel application of evidence ratio methods (Appendix A: Fig. A1). First, we calculated Akaike’s information criterion weights per model suite (Anderson and Burnham 2002, Wagenmakers and Farrell 2004). Then we calculated evidence ratios, with model comparisons within suites informed by observations of which predictor variables were found to be the most important for the top model across suites. This process does not compare AIC values across suites (Anderson and Burnham 2002); rather it compares those environmental factors most important per response variable. Evidence ratios > 10 were regarded as showing sufficient contrast (Uriarte et al. 2004).

Fitness based on isometric or allometric scaling

The first step toward linking habitat suitability with fitness is to connect the size of an individual with its reproductive effort (Niklas and Enquist 2003, Mróz and Kosiba 2011). Our approach was to test whether there is a linear relationship between reproductive effort (scape length in mm; estimated number of flowers) and lamina area in cm^2 (for the largest leaf per individual), based on measurements sampled from mature *P. stachyodes* located near the LFDP plot ($n = 30$). We expected a positive, linear relationship, and specifically tested whether the scaling was isometric, with reproductive effort proportionate to lamina area (a proxy for energy available from photosynthesis), or allometric (disproportionate energy cost). Under isometric scaling, scape length to lamina area has a predicted slope of $1/2$, because length is one-dimensional and lamina area is two-dimensional; and the estimated number of flowers to lamina area has a predicted slope of $3/2$, assuming flower arrangement within three-dimensional space.

To gain further perspective on the response variables used in the SDM, we also examined the relationship between physical size and abundance, with specific comparisons between size classes (potential life stages). Within sites with co-occurring orchids (>1), we selected the largest (most likely mature), and smallest (most likely immature) individuals and tested lamina area (cm^2) as a function of orchid density (number of plants/ m^2) per subplot. We then tested whether the slope of this relationship was comparable to the self-thinning rule

TABLE 1. Indicator species analysis for the terrestrial orchid *Prescottia stachyodes* terrestrial orchid in the Luquillo Forest, Puerto Rico.

Family	Species	Association	<i>P</i>		
			Entire plot	Cover class 1–3	Cover class 4
Malpighiaceae	<i>Byrsonima spicata</i> (Cav.) DC.	positive	...	0.025	...
Salicaceae	<i>Casearia arborea</i> (Rich.) Urb.	positive ±	0.027	0.005	...
Boraginaceae	<i>Cordia sulcata</i> DC.	positive	0.005
Myrtaceae	<i>Eugenia stahlia</i> (Kiaersk.) Krug and Urb.	positive ±	0.03	...	0.011
Moraceae	<i>Ficus citrifolia</i> Mill.	positive	0.024
Chrysobalanaceae	<i>Hirtella rugosa</i> Pers.	positive ±	0.036
Sapindaceae	<i>Matayba domingensis</i> (DC.) Radlk.	positive ±	0.011	0.001	...
Salicaceae	<i>Casearia sylvestris</i> Sw.	negative ±	0.018	0.018	...
Sapotaceae	<i>Manilkara bidentata</i> (A. DC.) A. Chev.	negative	0.016

Notes: Results are based on the presence or absence of *P. stachyodes* and the basal area of 118 woody plants within the Luquillo Forest Dynamics Plot (LFDP). Analyses were conducted with PC-ORD. Significant results ($P < 0.05$) are shown for the entire LFDP plot, for areas with historic land use disturbance (cover class 1–3), and for the area with the least disturbance (cover class 4). Ellipses indicate that results are not significant. The symbol “±” indicates the same association as the orchid *Wulfschlaegelia calcarata* (Bergman et al. 2006).

(−3/2) used to describe size–density dynamics of trees (Yoda et al. 1963), or closer to −0.44, as observed with other herbaceous monocots (Weller 1987). Note that our metric for size was based on lamina area (cm²) rather than dry lamina biomass (g), due to restrictions on removing plant tissue; however, these two metrics tend to be highly correlated, with an expected scaling relationship close to 1 (Niklas et al. 2007). In terms of known allocation strategy, the majority of *P. stachyodes* biomass is composed of leaves, with few roots. We expected that higher densities of orchids would result in smaller-sized plants due to competition for resources.

We used the R package SMATR (Warton et al. 2012) to test whether observed slopes matched predictions inspired by ecological theory. Slopes (reproductive effort varying with plant size; plant size varying with density) were calculated using reduced major axis (RMA) regression, also known as standardized major axis (SMA) regression (Warton et al. 2006), after log₁₀-transformation of all data. We chose the RMA method based on our sample size and assumption of comparable measurement errors for both the *X* and *Y* axis. A significant difference in scaling (line-fit) was dependent upon nonoverlap of the predicted slope and the 95% confidence interval for the observed slope (Warton et al. 2006, 2012).

RESULTS

Orchid distribution and indicator species analysis

A total of 218 *P. stachyodes* were identified in 90 of 1200 (7.5%) of the 5 × 5 m subplots (Appendix D: Fig. D1). The largest leaf per individual had a mean lamina area of 52.8 ± SE 2.17 cm² (minimum 1.9 cm²; maximum 132.8 cm²). The average subplot density was 0.36 plants/m², with highest density recorded being 18 individuals (3.6 individuals/m²). Orchid presence displayed significant spatial autocorrelation ($P = 0.001$), with a pattern described as slightly clustered within a short distance (0–20 m), and then becoming random over longer distances (>20 m), with Moran's *I* statistic =

0.009 (where −1 is highly dispersed, 0 is random, and 1 is highly clustered). Smoothing methods (*X*, *Y* coordinates) were then used to reduce spatial autocorrelation for the residuals in the GAM model suite, with the change resulting in nonsignificant spatial autocorrelation for the null GAM model (Appendix E: Figs. E1 and E2). Within sites where orchids were present, spatial autocorrelation was nonsignificant; thus, no changes were made to the GLM and LM model suite. Orchid abundance was aggregated (using the index of clumping, or IC, where <0 is uniform, 0 is random, and >0 is clustered), with majority of individuals being restricted to a few sites for both 5 × 5 m subplots (IC = 4.5) and 20 × 20 m plots (IC = 8.4). A histogram of orchid abundance data is shown in Appendix F: Figs. F1 and F2.

There were relatively few indicator species (nine out of 118 species tested) associated with *P. stachyodes* presence relative to the overall plant diversity of the LFDP plot (Table 1). However, sites with >1 indicator species accounted for 71% (156 out of 218) of the total *P. stachyodes* sampled. Positive relationships were found with seven species, whereas negative relationships were found for two (Table 1).

Modeling orchid presence–absence, abundance, and size

The top generalized additive model (GAM) that we selected (Table 2; Appendix C: Table C1; Appendix G: Fig. G1) for predicting orchid occurrence included the following factors: indicator species (especially co-occurrence with positive indicator species) and areas with higher diffuse solar radiation residuals (locations with greater light availability, attributed to aspect rather than slope). Alternate top-ranking models (Appendix C: Table C1) also highlighted the importance of interactions between degree slope and topographic position (with orchid occurrence associated with the flat terrain on the tops of hills). The top GAM model selected had an AUC score of 0.854, where AUC of 0.5 is null (or random) and 1.0 is excellent (Hanley and McNeil 1983,

TABLE 2. Model coefficients for top models of orchid (*Prescottia stachyodes*) presence, abundance, and size in the Luquillo Forest Dynamics Plot, Puerto Rico, based on similarity between observed and predicted values, with Spearman's rank correlation ρ (predicted and observed), root mean square error (RMSE), and average error (AVE_{err}).

Model and predictor variable	Coefficient \pm SE	Spearman's ρ	RMSE	AVE_{err}
Top GAM, presence (1) and absence (0)		0.33***	-4.76	-3.96
(Intercept)	-5.37 \pm 0.68***			
Diffuse solar radiation (residuals from regression with slope)	0.04 \pm 0.02*			
Indicator species, both positive and negative	1.59 \pm 0.68*			
Indicator species, positive only	2.16 \pm 0.64***			
Indicator species, neither positive or negative	1.53 \pm 0.66*			
Top GLM, orchid abundance (count per subplot)		0.32**	2.42	<0.001
(Intercept)	1.11 \pm 0.23***			
Degree slope	-0.10 \pm 0.02***			
Native orchid, <i>Wulfschlaegelia calcarata</i>	-1.00 \pm 0.29***			
Soil type, Zarzal	-1.17 \pm 0.23***			
Top LM, largest individual per subplot (lamina area, cm ²)		0.39***	29.99	<0.001
(Intercept)	79.52 \pm 4.58***			
Rockiness	-25.04 \pm 6.72***			

Notes: Model rank was informed by Akaike's information criterion (AIC) and the Bayesian information criterion (BIC). Top models included (1) generalized additive models (GAM) of orchid presence-absence (with smoothing for X , Y coordinates and including all plots without missing data [$n = 1070$]); (2) generalized linear models (GLM) of orchid abundance; and (3) linear model (LM) for maximum plant size per plot (GLM and LM models were restricted to plots where orchids were present [$n = 88$]). For complete details on model design and predictor variable units, refer to *Methods*.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Pearce and Ferrier 2000). For evaluation of GAM top model accuracy, there was a significant correlation between predicted and observed values (Spearman's rank $\rho = 0.33$, $P < 0.001$), with a root mean square error (RMSE) of 4.76 and an average error (AVE_{err}) of -3.96, with observed units based on orchid presence (1) or absence (0) and predicted units as continuous values.

Within sites where orchids were present, the top generalized linear model (GLM) of zero-truncated orchid abundance included soil type (positive for Zarzal), degree slope (negative trend with steeper terrain), and the occurrence of *W. calcarata* (negative trend for co-occurrence), as shown in Table 2. A second, slightly more complex model (Appendix C: Table C2) also included higher diffuse solar radiation residuals (positive trend). For evaluation of GLM top model accuracy, there was a significant correlation between predicted and observed values (Spearman's rank $\rho = 0.32$, $P = 0.004$), with a root mean square error (RMSE) of 2.42 orchids and an average error (AVE_{err}) of 0 orchids. The negative relationship with *W. calcarata* was unexpected, but a post hoc comparison of sites with either species of native orchid present revealed minimal overlap; only 10% of *W. calcarata*'s occurrence, and 24% of *P. stachyodes*' occurrence, were within shared subplots ($\chi^2 = 7.123$, $P = 0.007$).

Rockiness was the single most important factor for the top linear model (LM) for maximum orchid size per plot (Table 2), with larger plants in less rocky areas. Other similarly ranked models (Appendix C: Table C3) also included either soil type (negative for Zarzal) or degree slope (negative trend). For LM top model evaluation, there was a significant correlation between predicted and observed values (Spearman's rank $\rho = 0.39$, $P < 0.001$), with a root mean square error (RMSE)

of 29.99 cm² and an average error (AVE_{err}) close to 0 cm², with units referring to orchid size.

Environmental factors most important for orchid abundance differed from those that influence plant size (based on evidence ratios within each suite), even though the two response variables were correlated and all data came from the exact same plots (Fig. 1, Table 2; Appendix A: Fig. A1; Appendix C: Tables C2 and C3). The GLM top model for orchid abundance (soil type, degree slope, *W. calcarata* occurrence) was different from the top LM equivalent with rockiness as the predictor variable, based on $\Delta\text{AIC} = 33.1$ and an AIC evidence ratio of >15.5 million (BIC evidence ratio of >1.4 million). The LM top model (rockiness) was different from the top GLM equivalent with soil type, degree slope, and *W. calcarata* occurrence as the predictors variables, based on $\Delta\text{AIC} = 5.80$, and an AIC evidence ratio of 18.21 (BIC evidence ratio of >202.12 million).

Allometric and isometric scaling of reproductive traits, size, and density

Average reproductive effort recorded for *P. stachyodes* ($n = 30$) was as follows (data reported as mean \pm SE): scape length 471.2 \pm 19.0 mm (minimum 279.0 mm; maximum 705.0 mm); number of flowers 105 \pm 6.5 flowers (minimum 50; maximum 175 flowers). The lamina area for the largest leaf per flowering plant was 104.08 \pm 6.63 cm² (minimum 43.91 cm²; maximum 183.59 cm²). Reproductive effort was significantly influenced by plant size (lamina area), based on scape length ($R^2 = 0.37$, $P < 0.001$) and estimated total number of flowers ($R^2 = 0.50$, $P < 0.001$) as response variables (Appendix B: Table B2; Appendix H: Figs. H1 and H2). The RMA slope estimates for reproductive

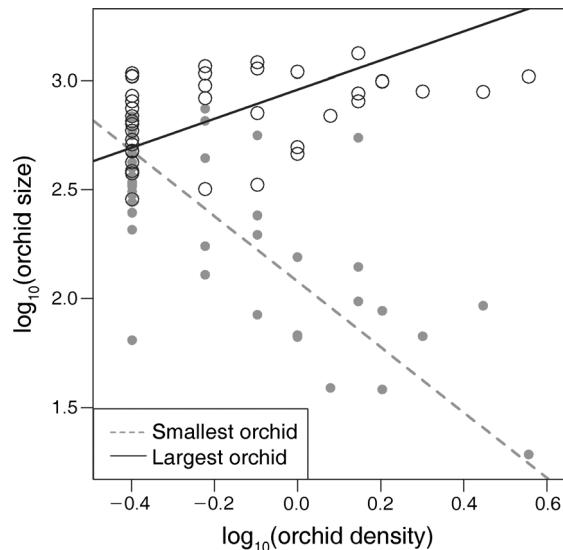


FIG. 2. Plant size as a function of density for the largest and smallest co-occurring orchids per subplot. Plant size was influenced by subplot density for the smallest ($P < 0.001$, $R^2 = 0.48$) and the largest ($P = 0.015$, $R^2 = 0.13$) plants. Lines show the reduced major axis (RMA) slope for \log_{10} -transformed size (lamina area in cm^2) varying with \log_{10} -transformed density (number of plants/ m^2). For the smallest individuals, slope = -1.5 (95% CI = -1.90 , -1.19); for the largest individuals, slope = 0.67 (95% CI = 0.49 , 0.90).

effort varying with plant size (Appendix B: Table B2) matched our isometric predictions for scape length ($P = 0.18$), but not for number of flowers ($P = 0.003$); scape had a slope of 0.62 (95% CI = 0.45 , 0.83 ; 0.5 predicted); total number of flowers had a slope of 0.98 (95% CI = 0.75 , 1.28 ; 1.33 predicted).

Plant size (lamina area) was influenced by subplot orchid density for both the smallest ($P < 0.001$, $R^2 = 0.48$) and the largest plants ($P = 0.015$, $R^2 = 0.13$; Fig. 2; Appendix B: Table B3), but not for the average of co-occurring individuals ($P = 0.75$). The reduced major axis (RMA) slope estimates for plant size varying with density for the smallest individuals was -1.5 (95% CI = -1.90 , -1.19), and was different from the predicted -0.44 scaling for herbaceous monocots ($P < 0.001$), but not different from the $-3/2$ self thinning rule ($P = 0.99$). Counter to expectations, the largest individuals had a positive slope of 0.67 (95% CI = 0.49 , 0.90) that was also significantly different than self-thinning predictions ($P = 0.008$, $P < 0.001$). As a post hoc analysis, we found that the sizes of the largest and smallest individuals were independent from one another, with no significant correlation ($P = 0.53$).

DISCUSSION

To date, the majority of species distribution modeling (SDM) techniques have focused on the identification of suitable habitat by using environmental conditions as predictors for species occurrence or abundance. Although this approach is effective for some applications,

there is growing interest in SDMs that offer a more mechanistic perspective on distribution patterns of an organism, often obtained by incorporating eco-physiological responses, biotic interactions, life history stages, or resource-allocation trade-offs (Guisan and Thuiller 2005, Kearney and Porter 2009, Douma et al. 2012, Lasky et al. 2014). Our approach to SDMs was to link habitat suitability with fitness differences via testing of allometric relationships (reproductive effort varying with plant size; plant size varying with density). Additional insights on our focal species were gained by adopting a two-part conditional modeling approach (suitable for instances of zero inflation), followed by informed comparisons of factors most important for species abundance in contrast to plant size. Thus, while exploring the local distribution complexities of a single species of orchid (*Prescottia stachyodes*), we have demonstrated novel SDM methods applicable to a broader audience of ecological researchers.

Insights on the complexity of orchid distribution and defining "suitable habitat"

The spatial distribution patterns of *P. stachyodes* (clustered occurrence at short spatial scales shifting to random occurrence with distance, combined with clumped abundance) are not surprising, given models of orchid seed dispersal patterns (Kindlmann et al. 2014), and field observations reported in both temperate and tropical habitats (e.g., Jacquemyn et al. 2007, Whitman et al. 2011). These spatial patterns are also common with tropical tree species (Condit et al. 2000) and may reflect either dispersal limitation or highly specific niche requirements (Brown et al. 1995). Overall, distribution patterns for *P. stachyodes* occurrence and abundance suggest that either most seeds are deposited near maternal plants, resulting in a hotspot for germination (Jacquemyn et al. 2007, Jersáková and Malinová 2007), or that sites for population establishment are spatially localized, which may be accompanied by strong competition for limiting resources (Otero et al. 2007, Bunch et al. 2013). The random patterns of *P. stachyodes* occurrence with distance may be due to chance long-distance dispersal events combined with the low probability of seeds landing on suitable habitat in a landscape of high physiographic, and perhaps mycorrhizal, heterogeneity. In addition, subpopulation persistence fluctuates through time, especially when mortality of seedlings and juveniles is high (Ackerman et al. 1996, Tremblay 1997, Otero et al. 2007).

Orchids are distinct from most other plants in that they must exploit fungi to successfully germinate. Thus, their distribution often reflects the extent of below-ground mycorrhizal fungi networks (Jacquemyn et al. 2007, Jersáková and Malinová 2007, McCormick et al. 2012). Our knowledge of tropical orchid–fungi relationships is limited, but the indicator species analysis results may provide useful insights on direct and indirect species interactions, suitable habitat niches, or edaphic condi-

tions that promote orchid germination or population establishment. The roots, or decomposing organic matter, associated with positive indicator species may help to facilitate mycorrhizal networks (Gowland et al. 2011, McCormick et al. 2012, Bunch et al. 2013), whereas negative indicator species may host pathogens or may excrete secondary compounds that inhibit the fungi upon which orchids rely (Bento et al. 2014). Within our study site, the mycoheterotrophic orchid *Wulfschlaegelia calcarata* is associated with nearly three dozen indicator species (Bergman et al. 2006), whereas *P. stachyodes* has fewer significant associations (or potentially more specialized relationships). However, the majority of *P. stachyodes* associations are comparable to those of *W. calcarata* (e.g., positive associations with the tree *Matayba domingensis* (DC.) Radlk. and negative with *Casearia sylvestris* (Rich.) Urb., a species with anti-fungal properties (Bento et al. 2014)).

The top generalized additive model (GAM) of orchid presence-absence reinforced the importance of indicator species and the need to consider both abiotic habitat characteristics and relationships with other plants, even if the underlying biotic interactions between species remain unknown. The significance of indicator species within the top generalized additive model could also be based on similarity of habitat needs, or across-species reliance on an environmental characteristic not explicitly included in our study (e.g., locations of canopy gaps, microclimate conditions, specific soil nutrients). The significance of diffuse solar radiation (residuals) is interpreted as representing hillside aspect, rather than degree slope, and highlights the need for more detailed information on understory light availability. Our findings complement the observation that light is a very limited resource (and thus of high importance) for plant species within dense subtropical forests (Comita et al. 2009).

Results from the generalized linear model (GLM) of orchid abundance supported some, but not all, of our a priori expectations. The edaphic bias of *P. stachyodes* toward Zarzal soil, described as very fine and moderately well drained (Vick and Lynn 1995), was not consistent with our predictions, but was comparable to prior findings by Cohen and Ackerman (2009). However, the negative influence of steep terrain (degree slope) on orchid abundance did match expectations and is most likely attributed to the shallow root system of *P. stachyodes*. The negative association with the native orchid *Wulfschlaegelia calcarata* was surprising, but may be the consequence of the preference of *P. stachyodes* for higher light situations than the non-photosynthetic *W. calcarata*, and most likely reflects unique habitat niches.

The linear model (LM) of plant size highlighted the influence of rockiness on *P. stachyodes* habitat needs for optimum growth. However, counter to our hypothesis, radiation and topographic position were not included in any of the highly ranked LMs; these factors are potentially more important for colonization or seedling

survival (hence inclusion in the top GAMs and GLMs). Our interpretation is that rockiness does not directly impact plant size, but rather it is indicative of habitat characteristics not explicitly measured. Areas with decreased rubble (rockiness) might create a microenvironment with deeper leaf litter between boulders, and thus a more robust fungal community for providing nutrients (McCormick et al. 2012). Density of neighboring herbs was an unexplored factor that could influence orchid vegetative traits (Givnish 1982), but this is unlikely because the understory of tabonuco forests is relatively sparse. The negative leaf size trend with Zarzal (within the alternate LM top model) could be attributed to the reduced water-holding characteristics, compared to poor drainage associated with Cristal soil (Vick and Lynn 1995).

Historic land use practices were not a significant factor for any of the top GAM, GLM, or LM models. The tolerance of *Prescottia stachyodes* for anthropogenic disturbance events is in sharp contrast to other studies within the Luquillo forest. For instance, Bergman et al. (2006) found that the native orchid *W. calcarata* was especially sensitive to anthropogenic disturbance events. Furthermore, historic canopy cover was also found to be the primary factor for shaping overall forest composition (Thompson et al. 2002).

New perspectives on orchid size

We found that the extra steps required to investigate fitness measures (i.e., reproductive effort, size-density relationships) provided a deeper understanding of overall orchid ecology and interpretation of SDM results. For instance, plant size (one of the SDM response variables) strongly influenced the reproductive effort of mature *P. stachyodes*, most likely because larger leaves produce more photosynthates that could be allocated toward reproduction. Also of interest was the differing “cost” of the reproductive structures examined. Scape length, the structural support needed to display flowers, was isometric, with a slope $\sim 2/3$ (as predicted), whereas the total number of flowers was allometric, with a slope ~ 1 (counter to our $3/2$ prediction), indicating a greater energy cost to the plant. Within a broader context, the slopes that we observed for individual reproductive parts (scape, number of flowers) differed from findings based on total reproductive and leaf biomass (Niklas and Enquist 2003), but the post hoc average of *P. stachyodes* reproductive results (0.80) was comparable to scaling trends observed across species (average 0.84, 95% CI = 0.78–0.90; Niklas and Enquist 2003). Overall, our results suggest potential life history trade-offs, such as energy toward new foliage vs. more flowers, when *P. stachyodes* are located within less optimal habitat or areas with fewer resources.

Prescottia stachyodes did not display the predicted (−0.44) self-thinning scaling exponent for herbaceous monocots (Weller 1987). Smaller orchids did display a strong negative size-density trend (nearest to a $-3/2$

slope), but more intriguing was the positive size–density slope (nearest to a 2/3 slope) for the largest orchids, combined with the lack of significant interaction between size classes. One explanation of these differing context-dependent size–density results is that areas with the highest orchid densities are distinct subpopulations (Tremblay et al. 2006) that include mixed age ranges, and that sites with the lowest orchid densities are older subpopulations (based on the intercepts; Fig. 2) that have been reduced to a few larger individuals that survive longer than smaller plants. When considering these size–density results under the context of SDMs, it appears that orchid abundance (density) is more attributed to habitat specificity (and potentially interspecific competition) than to intraspecific competition or resource partitioning (Goldberg and Barton 1992).

Linking habitat characteristics with possible life history stages

The overarching results from our study, that factors most important for orchid occurrence differ from those linked with abundance or plant size, suggest that the relevance of specific habitat characteristics may change over time or with life history stage. Habitat characteristics that promote larger sized *P. stachyodes*, and thus greater reproductive effort and eventual seed output, are not necessarily the same conditions needed for seedling establishment or the maintenance of subpopulations. Disjunction between habitat needs at different life stages is feasible, given the overall ecological complexity attributed to this taxonomic group (Givnish 1982, Jacquemyn et al. 2007, Whitman et al. 2011, Bunch et al. 2013). For instance, specificity of tree host substrate was not linked to adult orchid fitness or probability of flowering, but may be attributed to conditions necessary for early life stages (Gowland et al. 2011). Having spatial distribution patterns linked to a broad suite of habitat characteristics and belowground fungal associations, rather than governed by a single factor, also explains the rarity of some orchid species (Jersáková and Malinová 2007, Phillips et al. 2011, Bunch et al. 2013, McCormick and Jacquemyn 2014) and the potential ecological mechanisms that underlie distribution patterns of our model organism.

CONCLUSION

Environmental factors of importance in species distributions differ depending on how one identifies “suitable habitat” for a species. Had we restricted the scope of our analyses to more standard response variables used in species distribution modeling (e.g., presence-only data), or relied strictly on abiotic environmental data without exploring species diversity within this forest type, then we might not have sufficiently represented the ecological complexity of our model organism. Analyses of isometric, compared to allometric, scaling of reproductive effort, and size–density relationships, added valuable perspectives on potential fitness

differences, and possible population dynamics. Apparently, sites that are the source of seeds in *Prescottia stachyodes* may not be optimal for establishment. Thus, we conclude that habitat characteristics influencing species abundance can differ from conditions that influence plant size or reproductive effort.

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LITERATURE CITED

- Aarssen, L. W., and D. R. Taylor. 1992. Fecundity allocation in herbaceous plants. *Oikos* 65:225–232.
- Abramoff, M. D., P. J. Magalhaes, and S. J. Ram. 2004. Image processing with ImageJ. *Biophotonics International* 11:36–42.
- Ackerman, J. D. 1995. An orchid flora of Puerto Rico and the Virgin Islands. *Memoirs of the New York Botanical Garden* 73:1–208.
- Ackerman, J. D. 2014. Orchids of the Greater Antilles. *Memoirs of the New York Botanical Garden* 109:1–621.
- Ackerman, J. D., A. Sabat, and J. K. Zimmerman. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia* 106:192–198.
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723.
- Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912–918.
- Barry, S. C., and A. H. Welsh. 2002. Generalized additive modelling and zero inflated count data. *Ecological Modelling* 157:179–188.
- Bento, T. S., L. M. B. Torres, M. B. Fialho, and V. L. R. Bononi. 2014. Growth inhibition and antioxidative response of wood decay fungi exposed to plant extracts of *Casearia* species. *Letters in Applied Microbiology* 58:79–86.
- Bergman, E., J. D. Ackerman, J. Thompson, and J. K. Zimmerman. 2006. Land-use history affects the distribution of the saprophytic orchid *Wulfschlaegelia calcarata* in Puerto Rico’s tabonuco forest. *Biotropica* 38:492–499.
- Bjornstad, O. N. 2013. ncf: spatial nonparametric covariance functions. R package v 1.1-5. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/web/packages/ncf/index.html>
- Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics* 16:363–392.
- Brotions, L., W. Thuiller, M. Araújo, and A. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 4:437–448.
- Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. *Ecology* 76:2028–2043.

- Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo experimental forest. General Technical Report SO-44:1-132. USDA Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, USA.
- Bunch, W. D., C. C. Cowden, N. Wurzbarger, and R. P. Shefferson. 2013. Geography and soil chemistry drive the distribution of fungal associations in lady's slipper orchid, *Cypripedium acaule*. *Botany* 91:850-856.
- Cohen, I. M., and J. D. Ackerman. 2009. *Oeceoclades maculata*, an alien tropical orchid in a Caribbean rainforest. *Annals of Botany* 104:557-563.
- Comita, L. S., M. Uriarte, J. Thompson, I. Jonckheere, C. D. Canham, and J. K. Zimmerman. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology* 97:1346-1359.
- Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer, New York, New York, USA.
- Condit, R., et al. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288:1414-1418.
- Cornwell, W. K., and D. D. Ackerly. 2010. A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology* 98:814-821.
- Cragg, J. G. 1971. Some statistical models for limited dependent variables with application to the demand for durable goods. *Econometrica* 39:8829-8844.
- Cunningham, R. B., and D. B. Lindenmayer. 2005. Modeling count data of rare species: some statistical issues. *Ecology* 86:1135-1142.
- David, F. N., and P. G. Moore. 1954. Notes on contagious distributions in plant populations. *Annals of Botany* 18:47-53.
- Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609-628.
- Douma, J. C., J. M. Witte, R. Aerts, R. P. Bartholomeus, J. C. Ordoñez, H. O. Venterink, M. J. Wassen, and P. M. van Bodegom. 2012. Towards a functional basis for predicting vegetation patterns; incorporating plant traits in habitat distribution models. *Ecography* 35:294-305.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- ESRI. 2004. ArcGIS. Environmental Systems Research Institute, Redlands, California, USA.
- Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service Research Paper ITF-18. International Institute for Tropical Forestry, Rio Piedras, Puerto Rico, USA.
- Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, New York, New York, USA.
- Givnish, T. J. 1982. On the adaptive significance of leaf height in forest herbs. *American Naturalist* 120:353-381.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139:771-801.
- Gowland, K. M., J. Wood, M. A. Clements, and A. B. Nicotra. 2011. Significant phorophyte (substrate) bias is not explained by fitness benefits in three epiphytic orchid species. *American Journal of Botany* 98:197-206.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809-2815.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143:29-36.
- Hanley, J. A., and B. J. McNeil. 1983. A method of comparing the areas under receiver operating characteristic curves derived from the same cases. *Radiology* 148:839-843.
- Jacquemyn, H., R. Brys, K. Vandepitte, O. Honnay, I. Roldán-Ruiz, and T. Wiegand. 2007. A spatially explicit analysis of seedling recruitment in the terrestrial orchid *Orchis purpurea*. *New Phytologist* 176:448-459.
- Jersáková, J., and T. Malinová. 2007. Spatial aspects of seed dispersal and seedling recruitment in orchids. *New Phytologist* 176:237-241.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334-350.
- Kindlmann, P., E. Meléndez-Ackerman, and R. L. Tremblay. 2014. Disobedient epiphytes: colonization and extinction rates in a metapopulation contradict theoretical predictions based on patch connectivity. *Botanical Journal of the Linnean Society* 175:598-606.
- Lasky, J. R., M. Uriarte, V. K. Boukili, and R. L. Chazdon. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences USA* 111:5616-5621.
- Latimer, A. M., S. Banerjee, H. Sang, E. S. Mosher, and J. A. Silander. 2009. Hierarchical models facilitate spatial analysis of large data sets: a case study on invasive plant species in the northeastern United States. *Ecology Letters* 12:144-154.
- Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhner, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8:1235-1246.
- Mazerolle, M. J. 2013. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package v 1.35. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/web/packages/AICcmodavg/index.html>
- McCormick, M. K., and H. Jacquemyn. 2014. What constrains the distribution of orchid populations? *New Phytologist* 202:392-400.
- McCormick, M. K., D. Lee Taylor, K. Juhaszova, R. K. Burnett, D. F. Whigham, and J. P. O'Neill. 2012. Limitations on orchid recruitment: not a simple picture. *Molecular Ecology* 21:1511-1523.
- McCune, B., and M. J. Mefford. 1997. PC-ORD for Windows. Multivariate analysis of ecological data version 4.0. MjM Software Design, Gleneden Beach, Oregon, USA.
- Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37:17-23.
- Mróz, L., and P. Kosiba. 2011. Variation in size-dependent fitness components in a terrestrial orchid, *Dactylorhiza majalis* (Rchb.) Hunt et Summerh., in relation to environmental factors. *Acta Societatis Botanicorum Poloniae* 80:129-138.
- Müller, I., B. Schmid, and J. Weiner. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3:115-127.
- Niklas, K. J., E. D. Cobb, U. Niinemets, P. B. Reich, A. Sellin, B. Shipley, and I. J. Wright. 2007. "Diminishing returns" in the scaling of functional leaf traits across and within species groups. *Proceedings of the National Academy of Sciences USA* 104:8891-8896.
- Niklas, K. J., and B. J. Enquist. 2003. An allometric model for seed plant reproduction. *Evolutionary Ecology Research* 5:79-88.

- Otero, J. T., J. D. Ackerman, and P. Bayman. 2002. Diversity and host specificity of endophytic *Rhizoctonia*-like fungi from tropical orchids. *American Journal of Botany* 89:1852–1858.
- Otero, J. T., S. Aragón, and J. D. Ackerman. 2007. Site variation in spatial aggregation and phorophyte preference in *Psychilis monensis* (Orchidaceae). *Biotropica* 39:227–231.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225–245.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. Ecological niches and geographic distributions. *Monographs in Population Biology*. Volume 49. Princeton University Press, Princeton, New Jersey, USA.
- Phillips, R. D., M. D. Barrett, K. W. Dixon, and S. D. Hopper. 2011. Do mycorrhizal symbioses cause rarity in orchids? *Journal of Ecology* 99:858–869.
- Potts, J. M., and J. Elith. 2006. Comparing species abundance models. *Ecological Modelling* 199:153–163.
- R Development Core Team. 2013. R version 3.1. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Singer, R. B., and M. Sazima. 2001. The pollination mechanism of three sympatric *Prescottia* (Orchidaceae: Prescottinae) species in southeastern Brazil. *Annals of Botany* 88:999–1005.
- Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. Garcia-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- Tremblay, R. L. 1997. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). *Biotropica* 29:38–45.
- Tremblay, R. L., E. Meléndez-Ackerman, and D. Kapan. 2006. Do epiphytic orchids behave as metapopulations? Evidence from colonization, extinction rates and asynchronous population dynamics. *Biological Conservation* 129:70–81.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Fourth edition. Springer, New York, New York, USA.
- Vick, R. L., and W. Lynn. 1995. Order 1 soil survey of the Luquillo Long-Term Ecological Research Grid, Puerto Rico. Pages 1–92. United States Department of Agriculture, National Resource Conservation Service, Lincoln, Nebraska, USA.
- von Liebig, J. F. 1847. *Organic chemistry in its applications to agriculture and physiology*. Fourth edition. Taylor and Walton, London, UK.
- Wagenmakers, E.-J., and S. Farrell. 2004. AIC model selection using Akaike weights. *Psychonomic Bulletin and Review* 11: 192–196.
- Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. smatr 3—an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3: 257–259.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.
- Weller, D. E. 1987. A reevaluation of the $-3/2$ power rule of plant self-thinning. *Ecological Monographs* 57:23–43.
- Whitman, M., M. J. Medler, J. J. Randriamanandry, and E. Rabakonandrianina. 2011. Conservation of Madagascar's granite outcrop orchids: the influence of fire and moisture. *Lankesteriana* 11:55–67.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B* 73:3–36.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14:107–129.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–H are available online: <http://dx.doi.org/10.1890/14-0104.1.sm>