

Influence of community structure on the spatial distribution of critically endangered *Dicerandra immaculata* var. *immaculata* (Lamiaceae) at wild, introduced, and extirpated locations in Florida scrub

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Abstract Community structure at local scales is a major factor controlling population and community dynamics of plant species. *Dicerandra immaculata* Lakela var. *immaculata* (Lamiaceae) is a critically endangered plant known only from a few locations in scrub habitat in Florida. Using seven sites where populations of *D. immaculata* were wild, introduced, and/or extirpated, we sought to answer the following questions: (1) how do habitat characteristics at locations supporting wild *D. immaculata* plants vary from random locations within the same habitat; (2) how do habitat characteristics differ between wild and extirpated populations; and (3) how do habitat characteristics differ between wild and introduced populations? At locations of wild *D. immaculata*, community structure had fewer woody stems, shorter understory vegetation, lower percent canopy coverage, and lower percent ground cover of detritus than random locations and locations with extirpated *D. immaculata*. In addition, bare ground decreased at extirpated locations because other plant species expanded their coverage,

water saturation of the soil increased, diversity of shrubs decreased, and composition of the overstory changed compared to that of wild locations. Habitat characteristics associated with introduced plants were more similar to characteristics at randomly chosen locations than those with wild plants. However, introduced plants tended to occupy locations that had drier soil, a higher abundance of conspecifics, and a higher proportion of woody understory plants than that of random locations. Overall, gaps in the canopy and at ground level are likely essential for survival and recruitment of *D. immaculata*.

Keywords Soil moisture · Gap specialist · Lakela's mint · Habitat

Introduction

Loss of habitat is the most common threat to the survival of species worldwide (Wilcove et al. 1998; Venter et al. 2006). Efforts are being made to slow or stop loss of critical habitat, which includes identifying biodiversity hotspots with populations of many rare species (Myers et al. 2000). Biodiversity hotspots, which have high levels of habitat loss, support many of the estimated 60,000 plant species that remain unknown to science (Joppa et al. 2011). Community structure at local scales is a major factor controlling

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population and community dynamics of plants (e.g., Münzbergová 2005; Richardson and Hanks 2011), therefore understanding the preferred habitat of rare plant species within these hotspots is critical for their conservation.

Scrub habitat, which is shrubland on xeric sands (Menges 1999), is a hotspot for rare and endemic plants in Florida, USA (Christman and Judd 1990; Estill and Cruzan 2001). Most short-lived perennial plants in scrub habitat are gap specialists (Christman and Judd 1990; Petrů and Menges 2003) because the canopy of pine (*Pinus* spp.), oak (*Quercus* spp.), and sand hickory (*Carya floridana* Sarg.) historically was periodically top-killed by fire. Canopy openings allow populations of gap specialists to increase (Menges and Quintana-Ascencio 2004; Menges et al. 2006), whereas survival and reproduction of gap specialists decline with increasing time post-disturbance (Menges and Quintana-Ascencio 2004; Menges et al. 2006; Evans et al. 2008). Therefore, gap specialists in Florida scrub may be particularly sensitive to variation in characteristics of their habitat, especially density of competitors and canopy cover.

Four annual and five short-lived perennial mint species in the genus *Dicerandra* (Lamiaceae) are restricted to scrub habitats and sandhill vegetation primarily in Florida (Huck and Chambers 1997; Oliveira et al. 2007). Most species of *Dicerandra* have extremely small geographic ranges, and the habitats where these populations are endemic are being converted by urban and agricultural development (Zona and Judd 1986; Huck et al. 1989; Christman and Judd 1990; Estill and Cruzan 2001). *D. immaculata* Lakela var. *immaculata* (Lamiaceae) is a critically endangered short-lived perennial that is known only from scrub habitat along a 4.8 km length of the Atlantic Coastal Ridge in Indian River and St. Lucie Counties, FL (Nelson 1996). Very little is known about the biology and ecology of this species, and nothing has been reported in the primary literature about its preferred niche within scrub habitat.

Wild populations of *D. immaculata* persist at five of its historic sites in South Florida (St. Lucie and Indian River Counties), and one of these locations has been augmented with germplasm propagated at Bok Tower Gardens (Lake Wales, FL) as part of a program to conserve this species. However, many of these sites are not protected or properly managed for populations of *D. immaculata*, so large areas within these sites no

longer have any surviving individuals. Three populations of *D. immaculata* also were introduced at new sites in Florida (St. Lucie and Martin Counties) and were naturalized. Using seven sites where populations of *D. immaculata* were wild, introduced, and/or extirpated, we sought to answer the following questions: (1) how do habitat characteristics at locations supporting wild *D. immaculata* plants vary from random locations within the same habitat; (2) how do habitat characteristics differ between locations with wild or extirpated populations; and (3) how do habitat characteristics differ between locations with wild or introduced populations? Answering these questions will provide information on habitat characteristics that influence the spatial distributions of wild *D. immaculata*, habitat characteristics that influence local extirpation and information on fundamental and realized niche, respectively.

Methods

Study sites

Specific names and geographic locations of the sites are not given to protect the remaining populations of *D. immaculata*. The seven sites all have sandy, well-drained soil that is near neutral in pH (6.7–6.9). The sites contain Florida scrub habitat, characterized by a canopy of *Pinus clausa* (Chapm. Ex Engelm.) Vasey ex Sarg., *Quercus* spp., and *C. floridana*, a shrubby midstory, and open, sandy gaps in the understory. Specific information about the sites is given in Table 1, but we provide additional details here. We know from yearly monitoring of the population that *D. immaculata* was locally extirpated from a parcel of Site 1 sometime after December 2010. Hurricanes in 2004 and 2005 devastated the population at Site 2, which had numbered in the thousands of individuals. Site 2 has not been managed to maintain gaps, so the understory is becoming dense, and *D. immaculata* are located in small clumps scattered throughout the site. Plants have recently been locally extirpated from a parcel within Site 2. Site 3 is unmanaged and more plants historically occupied Site 3, but the majority was destroyed during construction of a bridge during 2007–2008. The introduced populations at Sites 5–7 were derived from apical cuttings from plants at Site 1. Hurricanes and construction projects adjacent to Site 5

Table 1 Seven sites in South Florida, USA used to characterize habitat associated with wild, introduced, and extirpated populations of *Dicerandra immaculata*

Site (owner)	Hectares (occupied by <i>D. immaculata</i>)	No. of individuals	Type of location			
			Wild	Introduced (no. introduced; year introduced)	Extirpated (hectares; year extirpated)	Random
1 (St. Lucie Co.)	4,047 (2.0)	1,000–5,000	x		x (1.1; 2011)	x
2 (St. Lucie Co.)	5.0 (unknown)	125	x		x (0.4; 2008)	x
3 (Private)	4.7 (unknown)	<100	x			x
4 (Indian River Co.)	37.6 (12.0)	600	x	x (304; 2007–2008)		x
5 (St. Lucie Co.)	120 (1.4)	475		x (1500; 2002–2009)		x
6 (USA)	418 (0.2)	210		x (314; 1991, 1995)		x
7 (USA)	418 (2.5)	813		x (700; 1991–92, 1995)		x

Habitat was characterized at 20 locations for each type of population within a site and also at 20 corresponding random locations

caused high mortality of plants, but yearly demography data indicate the population is self-sustaining (unpublished data). Sites 6 and 7 are on a single federally owned property, but we consider the populations distinct because they are not in proximity with each other.

Environmental measurements

We tested for differences in community structure among wild, random, introduced, and extirpated locations (hereafter “site” refers to the larger geographic area inhabited by a population, and “location” refers to a plot within a site used to characterize habitat) of *D. immaculata* by estimating the same environmental variables that have been used in earlier ecological studies of plants and to characterize plant community structure (Richardson et al. 2006; Mayberry and Elle 2009; Richardson and Hanks 2009, 2011; Sommers et al. 2011). Each random location was selected and marked by walking a randomly determined direction and number of paces (between 2 and 20 paces) from a wild or introduced plant and placing a flag at the location to be characterized. A relatively small number of paces were used to keep random locations within the same geographic area of the local population of *D. immaculata*. We measured the following parameters at each location ($N = 340$) in September 2012: (1) distance to the nearest overstory tree; (2) distance to the nearest woody shrub that was taller than *D. immaculata*; (3) number of

woody stems within a 1 m radius of the center of the mint plant or flag (not including the central mint plant, but including other *D. immaculata*, if present); (4) number of plant species within a 1 m radius (i.e., species richness); (5) number of *D. immaculata* within a 1 m radius, not including the central plant; (6) maximum height of the understory vegetation within a 1 m radius; (7) average depth of detritus in a 1 m² quadrat that was centered around the mint plant or flag; and relative abundance of ground cover types within a 1 m² quadrat in which we quantified (8) bare ground; (9) detritus; (10) grasses; (11) herbaceous plants (non-grasses); and (12) woody plants. We determined the relative abundance of ground cover types by calculating the area of each quadrat that they covered. This area was estimated visually and quantified by assigning units based on the following system (after Richardson and Hanks 2009): 0.5 (0–1 % of the total area of the quadrat), 3 (1–5 %), 15 (5–25 %), 37.5 (25–50 %), 62.5 (50–75 %), 85 (75–95 %), and 97.5 (95–100 %). We also identified the species of the nearest overstory tree and woody shrub and the type of detritus in the 1 m² quadrat. Detritus at each location was classified into one of seven groups (1) no detritus; (2) decaying leaves from herbaceous plants; (3) decaying leaves from broadleaf woody plants; (4) pine needles; (5) twigs; (6) branches; or (7) a mixture of two or more of the previous categories. We haphazardly selected approximately half the total locations to measure soil moisture (i.e., percent relative saturation) with a Kelway[®] soil pH and

moisture meter (Kel Instruments Co., Inc., Wyckoff, NJ) and canopy density with a spherical densitometer (Robert E. Lemmon, Forest Densimeters, Bartlesville, OK).

How do habitat characteristics at locations supporting wild *D. immaculata* plants vary from random locations within the same habitat?

We determined whether distance to the nearest overstory tree, number of woody stems within a 1 m radius, number of *D. immaculata* within a 1 m radius, maximum height of the understory vegetation within a 1 m radius, and the relative abundance of bare ground, leaf litter, and herbaceous plants within a 1 m² quadrat influenced the spatial distribution of wild *D. immaculata* by comparing habitat of 80 wild plants with 80 random locations across Sites 1–4 (Table 1) using Akaike's information criterion adjusted for small sample sizes (AIC_c), and Akaike weights (w_i ; Burnham and Anderson 2002). AIC_c models are informative only if relevant predictor variables are used (Anderson 2008), so we selected predictor variables for modeling that we thought would be most likely to explain differences between wild and random location. We used the linear form of this modeling and normal errors to identify the most parsimonious models from a set of candidate models. We used a square-root arcsine transformation on proportional data and either a square-root or a base-10 log transformation on other data to meet assumptions of normality prior to AIC_c analysis.

The ΔAIC_c value for each model is the level of empirical support relative to all models in the candidate set (see Anderson 2008): values of 0–2 indicate strong empirical support of the model, values 4–7 indicate weaker support, values 9–14 indicate little support, and values >14 indicate no support. The weight of each model is the probability that it is the best model, and it varies from 0 (no support) to 1 (complete support). The evidence ratio (Δ_i) is a quantitative measure of the strength of a model compared to the best model. Adjusted R^2 values indicate how well each model fits the data set and its relative efficacy as a tool for prediction. The relative importance of each predictor variable can also be calculated by summing the weight of each model in which the variable appears (Anderson 2008), and the relative importance varies

from 0 (no support) to 1 (complete support). Regression coefficients ($\pm\text{SE}$) indicate whether predictor variables are positively or negatively associated with the response variable (i.e., presence of *D. immaculata*).

We tested whether soil moisture and percent canopy coverage differed between wild and random locations using separate generalized linear mixed models (PROC GLIMMIX, SAS Institute 2011). We calculated the percent number of times six categories of overstory trees were the nearest tree to wild and random locations at Sites 1–4: (1) *C. floridana*; (2) *P. clausa*; (3) *Schinus terebinthifolius* Raddi; (4) *Sabal palmetto* (Walt.) Lodd.; (5) *Quercus* spp.; or (6) other. A χ^2 contingency test was used to determine whether the mean percentage of each category, calculated across the four sites, differed between wild and random locations. The nearest shrubs to wild and random locations were diverse, so we used a χ^2 contingency test to compare the mean percentages of only the four most abundant categories of shrubs between wild and random locations: (1) *Quercus* spp.; (2) *Ximenia americana* L.; (3) *Sideroxylon tenax* L.; and (4) *C. floridana*. Lastly, we calculated the percent number of times each of the seven categories of detritus was the dominant type at wild and random locations and then compared the mean percentages with a χ^2 contingency test.

How do habitat characteristics differ between locations with wild or extirpated populations?

We used the same analysis as previously described to determine which habitat features differed between the locations of extirpated and wild *D. immaculata* at Sites 1 and 2 (Table 1). However, we did not include branches as a category of detritus because branches were not present at wild or extirpated locations. In addition, the number of *D. immaculata* within a 1 m radius was not included in the AIC analysis. We included the number of *D. immaculata* in the previous AIC analysis because this species was present at wild and random locations (random locations were located within the geographic area occupied by populations of *D. immaculata*). However, extirpated locations inherently have no surviving *D. immaculata*, so this measurement undoubtedly varies between extirpated and wild locations.

How do habitat characteristics differ between locations with wild or introduced populations?

We used separate multiple logistic regression models to find the best model that characterized differences in habitat characteristics between introduced and wild locations and introduced and random locations (PROC LOGISTIC; SAS Institute 2011). Distance to the nearest overstory tree, number of woody stems within a 1 m radius, number of *D. immaculata* within a 1 m radius, maximum height of the understory vegetation within a 1 m radius, and the relative abundance of bare ground, leaf litter, herbaceous plants, and woody plants within a 1 m² quadrat were included in the initial global model. We then eliminated some predictor variables to reduce multicollinearity and used AIC values to choose the best model from among models using different subsets of the predictors (after Sommers et al. 2011). Random locations used for these analyses were from Sites 4–7 which is also where we characterized the habitat of introduced populations. However, wild and introduced populations of *D. immaculata* are often allopatric, so the locations used to compare habitat associated with these two types of populations were largely from different sites (Table 1). We used logistic regression for these analyses because logistic regression is more appropriate than AIC_c and other statistical analyses (Sommers et al. 2011) for determining whether two groups are different (i.e., Do introduced locations differ from wild or random locations?). AIC_c cannot determine whether two groups are different, but is

appropriate for determining why two groups are different, as in our previous comparisons between other types of locations in this study.

We tested whether soil moisture and percent canopy coverage differed between introduced, wild, and random locations using separate generalized linear mixed models, as previously described. We used separate χ^2 contingency tests, also previously described, to compare the nearest tree and shrub and type of detritus at introduced locations versus wild and random locations. However, for the comparison of shrubs, the four categories differed from our previous analyses and were (1) *Quercus* spp.; (2) *C. floridana*; (3) *Dodonaea viscosa* Jacq.; and (4) *Serenoa repens* (Bartram) J.K. Small.

Results

How do habitat characteristics at locations supporting wild *D. immaculata* plants vary from random locations within the same habitat?

Four models identifying differences in community structure between locations with wild *D. immaculata* and locations that were randomly selected had strong empirical support ($\Delta AIC_c < 2$; Table 2). The AIC_c model that had the greatest support indicated that *D. immaculata* was negatively associated with height of the understory vegetation, proportion of detritus, and number of woody stems and was positively associated with the number of *D. immaculata*. The most important predictor variables (i.e., in nearly every model that

Table 2 Best fit AIC_c models from 127 candidate models that explain differences in habitat of wild *Dicerandra immaculata* and random locations with seven explanatory variables: distance to the nearest tree, height of understory vegetation

within 1 m of the plant or random location, number of woody stems within 1 m, number of *D. immaculata* within 1 m, and proportion of the ground within 1 m² that was bare or covered with detritus or non-grass herbaceous plants

Model variables	K	Log (L)	ΔAIC_c	w_i	A_i	Adj. R^2
Height of understory vegetation (-0.02 ± 0.01), proportion of detritus (-0.18 ± 0.08), number of woody stems (-0.21 ± 0.08), number of <i>D. immaculata</i> (0.56 ± 0.08)	6	152.6	0.00	0.18	1.0	0.40
Proportion of detritus, number of woody stems, number of <i>D. immaculata</i>	5	151.2	0.55	0.14	1.3	0.40
Height of understory vegetation, proportion of detritus, proportion of herbaceous plants, number of woody stems, number of <i>D. immaculata</i>	7	153.0	1.35	0.09	2.0	0.40
Height of understory vegetation, proportion of herbaceous plants, number of woody stems, number of <i>D. immaculata</i>	6	151.6	1.81	0.07	2.6	0.40

The regression coefficient \pm SE is given in parentheses for each variable in the best supported model. K number of parameters in the model, w_i Akaike weights, A_i evidence ratio

Table 3 Best fit AIC_c models from 63 candidate models that explain differences in habitat of wild *Dicerandra immaculata* and extirpated locations with six explanatory variables: distance to the nearest tree, height of understory vegetation

within 1 m of the plant or random location, number of woody stems within 1 m, and proportion of the ground within 1 m² that was bare or covered with detritus or non-grass herbaceous plants

Model variables	K	Log (L)	ΔAIC _c	w _i	Δ _i	Adj. R ²
Height of understory vegetation (−0.53 ± 0.17), proportion of bare ground (0.38 ± 0.19), proportion of detritus (−0.43 ± 0.17), number of woody stems (−0.59 ± 0.10)	6	87.0	0.00	0.39	1.0	0.53
Height of understory vegetation, proportion of bare ground, proportion of detritus, proportion of herbaceous plants, number of woody stems	7	151.6	1.40	0.19	2.1	0.53
Height of understory vegetation, proportion of detritus, number of woody stems	5	84.9	1.79	0.16	2.4	0.52

The regression coefficient ± SE is given in parentheses for each variable in the best supported model. K number of parameters in the model, w_i Akaike weights, Δ_i evidence ratio

carried weight) were number of *D. immaculata* and woody stems ($\Sigma w_i = 0.97$ and 0.94 , respectively). The proportion of detritus and height of the understory vegetation may be moderately important predictor variables because these variables carried a moderate weight ($\Sigma w_i = 0.62$ and 0.58 , respectively). The proportion of herbaceous plants, proportion of bare ground, and distance to the nearest tree are relatively unimportant variables for explaining the difference between habitat at wild and random locations because these variables carried little to no weight ($\Sigma w_i = 0.38$, 0.29 , and 0.01 , respectively).

Soil moisture did not differ between wild and random locations: percent relative saturation averaged only $\sim 3.5\%$ across both types of locations ($F = 0.67$, $df = 1,109$, $P = 0.42$). However, percent canopy coverage was $44 \pm 4\%$ at wild locations, which was lower than canopy coverage at random locations ($61 \pm 5\%$; $F = 7.27$, $df = 1,109$, $P = 0.008$).

The type of nearest tree and shrub did not differ between wild and random locations (tree, $\chi^2 = 7.20$, $df = 5$, $P = 0.21$; shrub, $\chi^2 = 0.86$, $df = 3$, $P = 0.84$). *C. floridana* was the most abundant tree nearest to wild and random locations ($>38\%$ of the locations). *Quercus* spp. were the most abundant shrub nearest to wild and random locations ($>45\%$ of the locations). However, the type of detritus differed between wild and random locations ($\chi^2 = 22.7$, $df = 6$, $P < 0.001$). Wild *D. immaculata* plants and random locations most often had a mixture of detritus within 1 m², but mixtures were less common at wild sites than random sites (45 vs. 65% of locations, respectively), whereas pine needles (15 vs. 0% , respectively) or no detritus (19 vs. 13% , respectively) was more common.

How do habitat characteristics differ between locations with wild or extirpated populations?

Three models identifying differences in habitat between populations of extirpated and wild *D. immaculata* had strong empirical support ($\Delta AIC_c < 2$; Table 3). The AIC_c model that had the greatest support indicated that *D. immaculata* was negatively associated with height of the understory vegetation, proportion of detritus, and number of woody stems and was positively associated with the proportion of bare ground. This means that extirpated locations have taller understory vegetation, a greater abundance of woody stems, a higher proportion of detritus, and lower proportion of bare ground than wild locations. The most important predictor variables were number of woody stems, height of the understory vegetation, and proportion of detritus ($\Sigma w_i = 0.98$, 0.96 , and 0.92 , respectively). The proportion of bare ground was a moderately important predictor variable ($\Sigma w_i = 0.66$), whereas the proportion of herbaceous plants and distance to nearest tree are relatively unimportant ($\Sigma w_i = 0.30$ and 0.08 , respectively).

Extirpated locations had higher soil moisture than that of wild locations ($3.3 \pm 0.8\%$ relative saturation vs. $1.1 \pm 0.4\%$, respectively; $F = 4.57$, $df = 1,65$, $P = 0.036$) as well as higher percent canopy coverage ($75 \pm 4\%$ canopy coverage vs. $57 \pm 5\%$, respectively; $F = 8.62$, $df = 1,65$, $P = 0.005$). The type of nearest shrub and tree differed between wild and extirpated locations (shrub, $\chi^2 = 26.2$, $df = 3$, $P < 0.001$; tree, $\chi^2 = 41.2$, $df = 5$, $P < 0.001$). *Quercus* spp. were the most abundant shrub nearest to extirpated locations, whereas the types of shrubs

Table 4 Relative frequency (\pm SEM) that shrub and tree species were nearest to locations of wild *Dicerandra immaculata* and extirpated locations and relative frequency (\pm SEM) that six categories of detritus were present at these locations

across two sites in Southern Florida. Frequencies within a row do not sum to 100 % for shrubs because other types of shrubs also were present, but not included

Location	Shrub species					
	<i>Quercus</i> spp.	<i>Ximenia americana</i>	<i>Sideroxylon tenax</i>	<i>Carya floridana</i>		
Wild	50 (5)	10 (5)	8 (8)	5 (0)		
Extirpated	90 (5)	3 (3)	0 (0)	0 (0)		
	Tree species					
	<i>Carya floridana</i>	<i>Pinus clausa</i>	<i>Schinus terebinthifolius</i>	<i>Sabal palmetto</i>	<i>Quercus</i> spp.	Other
Wild	35 (10)	33 (18)	13 (13)	8 (8)	8 (8)	5 (5)
Extirpated	55 (40)	3 (3)	10 (10)	20 (20)	13 (13)	0 (0)
	Detrital category					
	No detritus	Leaves of herbs	Leaves of broadleaf woody plants	Pine needles	Twigs	Mixture of detritus
Wild	5 (5)	3 (3)	15 (10)	23 (7.5)	5 (0)	50 (5)
Extirpated	0 (0)	5 (5)	0 (0)	0 (0)	0 (0)	95 (5)

found near wild locations were more diverse (Table 4). *C. floridana* and *S. palmetto* were more abundant in the overstory near extirpated locations compared to those of wild locations, whereas *P. clausa* was less abundant (Table 4). The type of detritus at wild and extirpated locations also differed ($\chi^2 = 127.2$, $df = 5$, $P < 0.001$): extirpated locations were likely only to have a mixture of detritus, whereas 50 % of the wild locations had only one type of detritus (Table 4). Pine needles were the most common individual type of detritus at wild locations (Table 4).

How do habitat characteristics differ between locations with wild or introduced populations?

Community structure around introduced populations differed from structure around wild populations of *D. immaculata* in terms of distance to the nearest tree, number of mint plants, and proportion of bare ground, detritus, herbaceous plants, and woody plants (Table 5). The most significant difference in habitat occupied by the two types of populations was the proportion of detritus: introduced locations had 31 % more detritus than wild locations within a 1 m² quadrat. Fewer habitat characteristics differed between introduced locations of *D. immaculata* and

random locations and included height of the understory vegetation, number of *D. immaculata*, and proportion of woody plants (Table 6). The most significant difference between introduced and random locations was the number of *D. immaculata* because few were present in random locations. The proportion of woody plants was the second most significant difference: introduced plants had 61 % more woody plants within 1 m² than that of random locations.

Locations with introduced *D. immaculata* did not differ from wild *D. immaculata* or random locations in percent canopy coverage ($F = 1.23$, $df = 2, 183$, $P = 0.30$). However, locations with introduced *D. immaculata* had lower mean soil moisture (0.68 ± 0.26 relative saturation) than wild (3.63 ± 1.14) and random (2.77 ± 0.66) locations ($F = 8.13$, $df = 2, 167$, $P < 0.001$). The type of nearest shrub, nearest tree, and detritus differed between introduced and wild locations of *D. immaculata* (shrub, $\chi^2 = 27.1$, $df = 3$, $P < 0.001$; tree, $\chi^2 = 33.3$, $df = 5$, $P < 0.001$; detritus, $\chi^2 = 16.5$, $df = 6$, $P = 0.01$). The type of detritus also differed between introduced and random locations, but the nearest shrub and tree did not (tree, $\chi^2 = 10.6$, $df = 5$, $P = 0.06$; shrub, $\chi^2 = 1.75$, $df = 3$, $P = 0.63$; detritus, $\chi^2 = 22.6$, $df = 6$, $P < 0.001$). *Quercus* spp. were the most common shrubs nearest to wild locations, whereas the shrubs nearest to introduced and random locations were more

Table 5 Best supported model from logistic regression analysis of habitat characteristics at introduced and wild locations of *Dicerandra immaculata* and the means (\pm SEM) for the habitat characteristics at each type of location

Habitat characteristic	Coefficient (SE)	Wald χ^2	<i>P</i>	Introduced locations	Wild locations
Distance to tree (cm)	0.003 (0.002)	4.31	0.038	105.0 (12.9)	94.6 (14.1)
Number of <i>D. immaculata</i>	−0.059 (0.030)	3.96	0.047	4.14 (0.45)	10.8 (2.31)
Proportion of bare ground	0.056 (0.022)	6.35	0.012	32.5 (3.22)	42.9 (3.39)
Proportion of detritus	0.077 (0.023)	11.1	<0.001	39.5 (3.32)	27.1 (2.91)
Proportion of herbaceous plants	0.077 (0.031)	6.24	0.013	4.70 (1.38)	4.13 (0.85)
Proportion of woody plants	0.068 (0.024)	8.09	0.004	24.3 (2.61)	23.1 (2.19)

Table 6 Best supported model from logistic regression analysis of habitat characteristics at introduced and random locations of *Dicerandra immaculata* and the means (\pm SEM) for the habitat characteristics at each type of location

Habitat characteristic	Coefficient (SE)	Wald χ^2	<i>P</i>	Introduced locations	Random locations
Height of understory vegetation (cm)	0.015 (0.007)	4.35	0.037	58.6 (3.55)	67.4 (5.45)
Number of <i>D. immaculata</i>	−0.817 (0.169)	23.4	<0.001	4.14 (0.45)	0.30 (0.22)
Proportion of woody plants	−0.027 (0.012)	5.14	0.023	24.3 (2.61)	9.49 (1.85)

diverse: the mean percentages of all three of the other shrub categories increased (Table 7). *P. clausa* was the most common tree nearest to introduced and random locations, whereas *C. floridana* was the most common tree nearest to wild locations (Table 7). Detritus was most likely to be a mixture at introduced, wild, and random locations, but the second most common type of detritus was pine needles, no detritus, or broad-leaf leaves from woody plants at introduced, wild, and random locations, respectively (Table 7).

Discussion

How do habitat characteristics at locations supporting wild *D. immaculata* plants vary from random locations within the same habitat?

Wild *D. immaculata* tend to grow in proximity to conspecifics. Our sampling cannot determine the type of dispersion, but it appeared clumped. The spatial distribution of *D. immaculata* makes studying habitat associations more difficult because we cannot determine whether plants are in their fundamental or realized niche. *D. immaculata* cannot reproduce asexually, so growing in proximity or clumps may indicate that seed dispersal is limited by intrinsic or extrinsic factors (Eriksson and Ehrlén 1992; Orrock et al. 2006) and/or that suitable habitat is limiting

(Graae et al. 2011; Dybzinski and Tilman 2012). We suspect that poor seed dispersal and lack of suitable habitat resulted in the distribution of *D. immaculata*. Seedlings in gardens at Bok Tower Gardens and in natural habitat are rarely located far from parent plants even though seemingly suitable habitat is vacant elsewhere within the site (unpublished data). However, in this study, random locations differed from locations with wild *D. immaculata* in important ways, revealing habitat characteristics that may render surrounding areas unsuitable for establishment, growth, and reproduction of *D. immaculata*.

We infer from differences in habitat between wild and random locations that the spatial distribution of *D. immaculata* may be restricted primarily by interference from taller woody plants. Competition has a strong influence on community structure of plants (Goldberg and Barton 1992), and neighboring plants may restrict sunlight (Ware 1991), space, nutrients or water (Aerts 1999), produce chemicals that inhibit growth and recruitment (Gómez-Aparicio and Canham 2008), influence rates of pollination, and/or produce debris that restricts growth and recruitment of an individual plant (Xiong and Nilsson 1999). Other species in the genus *Dicerandra*, including *D. frutescens* Shinners, *D. christmanii* R.B. Huck and W.S. Judd., and *D. immaculata* Lakela var. *savannarum* Huck, are believed to be gap specialists because they are more abundant in habitats that are sunnier and have

Table 7 Relative frequency (\pm SEM) that shrub and tree species were nearest to locations of wild and introduced *Dicerandra immaculata* and random locations across four sites in Southern Florida

Location	Shrub species						
	<i>Carya floridana</i>	<i>Dodonaea viscosa</i>	<i>Serenoa repens</i>	<i>Quercus</i> spp.			
Introduced	16 (11)	16 (16)	10 (6)	24 (6)			
Wild	10 (7)	0 (0)	3 (3)	45 (11)			
Random	15 (9)	10 (6)	8 (5)	28 (6)			
	Tree species						
	<i>Pinus clausa</i>	<i>Carya floridana</i>	<i>Schinus terebinthifolius</i>	<i>Sabal palmetto</i>	<i>Quercus</i> spp.	Other	
Introduced	55 (16)	8 (6)	30 (12)	7 (5)	1 (1)	0 (0)	
Wild	24 (9)	4 (4)	41 (7)	13 (6)	15 (5)	4 (2)	
Random	45 (18)	4 (2)	30 (10)	13 (5)	8 (8)	1 (1)	
	Detrital category						
	No detritus	Leaves of herbs	Leaves of broadleaf woody plants	Pine needles	Twigs	Branches	Mixture of detritus
Introduced	8 (3)	0 (0)	19 (7)	33 (13)	8 (4)	0 (0)	33 (6)
Wild	19 (6)	1 (1)	14 (4)	15 (6)	5 (0)	0 (0)	1 (1)
Random	11 (6)	7 (4)	22 (8)	21 (11)	0 (0)	4 (2)	37 (8)

Relative frequency (\pm SEM across four sites) that six categories of detritus were present at locations of wild and introduced *D. immaculata* and random locations. Frequencies within a row do not sum to 100 % for shrubs because other species of shrubs also were present, but not included. Introduced locations are significantly different from wild locations in nearest shrub, tree, and detrital category and also significantly different from random location in detrital category

a lower amount of leaf litter (Menges 1992; Evans et al. 2008; Peterson et al. unpublished data), therefore, access to sunlight might be one of the main mechanisms underlying the spatial distribution of *D. immaculata*.

How do habitat characteristics differ between locations with wild or extirpated populations?

Comparing locations where *D. immaculata* is extant versus extirpated identified specific habitat characteristics that may have changed over time to influence local extirpation of plants. Similar to random locations, extirpated locations had a greater number of woody stems, taller understory vegetation, higher percent canopy coverage, and higher percentage of the ground covered with detritus than wild locations. In addition, bare ground decreased in extirpated locations, water saturation of the soil increased, the diversity of shrubs decreased and became dominated by *Quercus* spp., *P. clausa* decreased in the overstory and *C. floridana* and *S.*

palmetto increased, and pine needles in the detrital layer decreased compared to those in the wild locations. These results support our prior conclusion that taller plants are outcompeting *D. immaculata*. However, these results also suggest that certain species of taller plants may allow for coexistence of *D. immaculata*, whereas others do not. *Quercus* spp., *C. floridana*, and *S. palmetto* may have a denser canopy than *P. clausa*, allowing less sunlight to reach *D. immaculata*. The debris produced by *Quercus* spp., *C. floridana*, and *S. palmetto* also tends to be coarser than that produced by *P. clausa* (personal observation) and may interfere with mature or seedling *D. immaculata*.

How do habitat characteristics differ between locations with wild or introduced populations?

Some habitat characteristics at locations where *D. immaculata* were introduced were similar to habitat supporting wild *D. immaculata*, but habitat of introduced plants was more similar to habitat at random

locations. This similarity could be attributed to the fact that introduced and random locations were sampled within the same sites and wild locations were sampled primarily from different sites (i.e., more variation in habitat between sites than within sites). The habitat characteristics associated with introduced plants also could largely be a result of how and where they were planted within sites. Introduced plants may not differ in many ways from random locations because the habitat preferences for this species were unknown at the time of planting, so individual plants may have been randomly placed within the habitat. However, introduced plants also may have associations with specific habitat characteristics, such as *P. clausa* if they were non-randomly planted near these characteristics. Random and directed planting are not mutually exclusive: the planting regime may have been random with respect to some habitat characteristics and directed with respect to others. The planting regime coupled with poor dispersal of seedlings and a wider tolerance to environmental conditions than previously assumed, could explain why introduced plants persist in habitat that differs from habitat of wild plants.

Conclusion

Understory plants in Florida scrub often respond negatively to an increase in shrub and litter cover (e.g., Quintana-Ascencio and Morales-Hernandez 1997; Menges et al. 2006), and *D. immaculata* appears to be no exception. Unsuitable habitat that has resulted mainly from suppressing wildfires may be limiting the distribution of *D. immaculata*. Loss of habitat is the most common threat to the survival of species worldwide, and suppression of fire is one mechanism that may result in loss of habitat for fire-dependent species. Virtually all wildfires in North America in the first half of the twentieth century were considered detrimental and were actively suppressed. As a consequence of fire suppression, many ecosystems are now in relatively long-unburned conditions, which has the potential to alter community composition in these ecosystems (e.g., Myers 1985; Abrams 1992) and reduce reproductive efforts by plant species (e.g., Pyke GH 1983; Ostertag and Menges 1994). Access to sunlight provided by gaps in the canopy and low competition from larger woody shrubs at ground level are likely essential for survival and recruitment of *D.*

immaculata in its native range. Gap habitat for *D. immaculata* and other specialists of Florida scrub may be created and maintained through prescribed burning and/or mechanical removal of competing plants. Future research should investigate specific habitat characteristics that impact the fitness and population dynamics of *D. immaculata* and the best management techniques to maintain these characteristics.

Future research also should explore whether populations of *D. immaculata* are seed-limited because our results from introduced populations indicate that the realized niche is narrower than the fundamental niche. Seed-limited populations have fewer individuals than the habitat can support because very few seeds are produced or because the seeds that are produced fail to reach potential recruitment sites (Eriksson and Ehrlén 1992; Svenning and Wright 2005). If wild populations of *D. immaculata* are seed-limited and do indeed have a wider fundamental niche than currently realized, then an effective strategy to increase population size would be to introduce seeds and cuttings into acceptable unoccupied habitat.

Our study was observational and cannot determine mechanisms that influence the spatial distribution of *D. immaculata*. Field assays with *D. immaculata* are needed to examine the extent to which recruitment into populations is limited by seed or habitat, followed by studies to examine the specific mechanisms that cause seed or habitat limitation. Populations of plants are often limited by seed and habitat, and the limiting mechanisms need to be identified to conserve rare plant species.

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