

# Urbanized landscapes favored by fig-eating birds increase invasive but not native juvenile strangler fig abundance

TREVOR CAUGHLIN,<sup>1,2,3</sup> JESSICA H. WHEELER,<sup>2</sup> JILL JANKOWSKI,<sup>1,4</sup> AND JEREMY W. LICHSTEIN<sup>1</sup>

<sup>1</sup>Department of Biology, University of Florida, P.O. Box 118525, Gainesville, Florida 32611 USA

<sup>2</sup>Environmental Studies Program, New College of Florida, 5800 Bay Shore Road, Sarasota, Florida 34243 USA

**Abstract.** Propagule pressure can determine the success or failure of invasive plant range expansion. Range expansion takes place at large spatial scales, often encompassing many types of land cover, yet the effect of landscape context on propagule pressure remains largely unknown. Many studies have reported a positive correlation between invasive plant abundance and human land use; increased propagule pressure in these landscapes may be responsible for this correlation. We tested the hypothesis that increased rates of seed dispersal by fig-eating birds, which are more common in urban habitats, result in an increase in invasive strangler fig abundance in landscapes dominated by human land use. We quantified abundance of an invasive species (*Ficus microcarpa*) and a native species (*F. aurea*) of strangler fig in plots spanning the entire range of human land use in South Florida, USA, from urban parking lots to native forest. We then compared models that predicted juvenile fig abundance based on distance to adult fig seed sources and fig-eating bird habitat quality with models that lacked one or both of these terms. The best model for juvenile invasive fig abundance included both distance to adult and fig-eating bird habitat terms, suggesting that landscape effects on invasive fig abundance are mediated by seed-dispersing birds. In contrast, the best model for juvenile native fig abundance included only presence/absence of adults, suggesting that distance from individual adult trees may have less effect on seed limitation for a native species compared to an invasive species undergoing range expansion. However, models for both species included significant effects of adult seed sources, implying that juvenile abundance is limited by seed arrival. This result was corroborated by a seed addition experiment that indicated that both native and invasive strangler figs were strongly seed limited. Understanding how landscape context affects the mechanisms of plant invasion may lead to better management techniques. Our results suggest that prioritizing removal of adult trees in sites with high fig-eating bird habitat may be the most effective method to control *F. microcarpa* abundance.

**Key words:** biological invasion; bird dispersal; *Ficus microcarpa*; Florida, USA; invasive and native fig species; inverse model; propagule pressure; seed addition experiment; seed dispersal; seed limitation; urbanization.

## INTRODUCTION

Propagule pressure, which reflects both seed production and dispersal, can have major impacts on plant population and community dynamics. Many of the processes that motivate interest in propagule pressure, such as regional beta-diversity, range expansion of invasive species, and metapopulation dynamics, occur at large scales and encompass a variety of land cover types (Condit et al. 2002, Levine and Murrell 2003, Simberloff 2009). Landscape context, defined here as the proportion of different land cover types in a landscape, and the spatial distribution of propagule sources in

relation to land cover, could change the strength of propagule pressure, with consequences for plant distribution and abundance. Seed dispersal by animals may be particularly dependent upon landscape context, because landscape composition and configuration can affect animal movement and abundance, potentially changing both seed dispersal distances and removal rates (Buckley et al. 2006, Uriarte et al. 2011). However, few studies have quantified how landscape context might alter seed dispersal, causing increases or decreases in propagule pressure in different landscapes.

Propagule pressure is particularly crucial for invasive species range expansion. Propagule addition experiments reveal that propagule input is often a stronger determinant of invasion success than microhabitat characteristics, including patch biodiversity and disturbance regime (Levine 2000, Von Holle and Simberloff 2005). However, if favorable microhabitats for recruitment are limited, propagule addition may increase invader abundance only if propagules arrive in favorable

Manuscript received 29 September 2011; revised 6 February 2012; accepted 8 February 2012. Corresponding Editor: R. T. Corlett.

<sup>3</sup> E-mail: trevor.caughlin@gmail.com

<sup>4</sup> Present address: Biodiversity Research Center, University of British Columbia, 6720 University Blvd., Vancouver, BC V6T 1Z4 Canada.

microhabitats (Britton-Simmons and Abbott 2008). Propagule addition studies are usually constrained to a small number of habitats, sometimes a single forest type. However, range expansion of invasive species often occurs over multiple landscapes, from introduction sites in human-inhabited areas to recruitment sites in undisturbed forest. Furthermore, although propagule addition experiments have provided insights into the roles of propagule pressure and microhabitat characteristics at small spatial scales, we lack an understanding of how landscape-scale habitat characteristics affect propagule pressure and invasion success.

Variation in human land use is a component of landscape context with the potential to alter the impact of propagule pressure on plant invasion. Many studies have coupled land-use data sets with mapped distributions of invasive plants to reveal a positive correlation between human disturbance and invasive species abundance (Burton et al. 2005, Bradley and Mustard 2006, Seabloom et al. 2006). However, these large-scale observational studies are usually unable to identify the mechanism behind this correlation, which could be explained by several different biological hypotheses. Intrinsic characteristics of habitats with high human land use, such as increased light and nutrient availability, could increase establishment of invasive species regardless of propagule pressure (Leishman and Thomson 2005). Alternatively, propagule pressure could increase in human-dominated landscapes due to increased abundance of reproductive individuals of invasive species deliberately planted by people (Colautti et al. 2006). Finally, human land use could amplify propagule pressure by increasing seed dispersal distances in disturbed landscapes (With 2002). Distinguishing among these hypotheses has implications for management of invasive species, because restricting propagule input requires different actions than manipulating environmental conditions to decrease survival of established plants (Reaser et al. 2007).

In Florida, native and invasive strangler figs (*Ficus aurea* and *F. microcarpa*, respectively; hereafter, "figs") provide an unusually tractable system for understanding how propagule pressure and landscape context influence the distribution of an invasive species. In Florida, seedling figs establish primarily in the canopy of a single species of common native palm, the cabbage palm (*Sabal palmetto*). As the figs reach maturity, they eventually become rooted in the ground. Consequently, suitable sites for seedling establishment are different than suitable sites for adult growth and survival, and the relationship between juvenile fig abundance in cabbage palms and adult fig abundance in soil is more likely to be influenced by seed dispersal than habitat effects on growth and survival. *F. aurea* and *F. microcarpa* have similar habitat preferences, growth forms, and dispersal mode, but *F. microcarpa* is in the process of rapid range expansion (Gordon 1998), whereas *F. aurea* is common throughout South Florida (Serrato et al. 2004). As a

result, comparing the two species provides a rare opportunity to explore how the spatial distribution of adult trees may affect propagule pressure and, ultimately, juvenile abundance.

Invasive fig abundance appears to be positively correlated with urban land use in Florida (EDDMapS 2011). We hypothesized that increased juvenile *F. microcarpa* abundance in urban landscapes can be explained by increased seed dispersal due to a higher abundance of seed-dispersing birds in urban environments. We also considered two alternative hypotheses: that presence of reproductive adults increases juvenile fig abundance regardless of human land use, and that human land use affects fig abundance by increasing juvenile fig survival. Additionally, we predicted that in our study area, which is within the established range of *F. aurea* but on the range boundary of *F. microcarpa*, dispersal limitation (and hence the degree to which the spatial distribution of juveniles is associated with adult locations) would be greater for the latter species. We tested these hypotheses by modeling juvenile fig abundance in relation to adult fig abundance and landscape-scale habitat suitability for fig-eating birds. To better understand the mechanisms behind our model results, we conducted a seed addition experiment. Our study bridges the knowledge gap between large-scale observational studies relating land cover to invasive plant abundance and more mechanistic propagule addition studies limited to small spatial scales. Consequently, we are able to provide novel insight into how landscape context may alter propagule pressure and, ultimately, the abundance of an invasive species in different landscapes.

## MATERIALS AND METHODS

### *Study region*

Our study region is located on the west coast of South Florida (Fig. 1). Existing figs were surveyed in plots across a 250-km transect from Anne Marie Island (27.471 N, 82.689 W) to Chokoloskee Island (25.838 N, 81.380 W), and the seed addition experiment was conducted at the northern edge of this transect in Sarasota (27.382 N, 82.564 W). The average annual precipitation for five sites within the 250-km transect is 1314 mm, and the average temperature is 23.2°C. The study region encompasses a range of natural habitats, including longleaf pine forest, mangrove swamp, and dry prairie. Invasive plant species are considered a major conservation threat in the region (Gordon 1998).

### *Study species*

*Ficus aurea* and *F. microcarpa* (see Plate 1) are the most common fig species in Florida and share a similar niche, with the majority of juvenile figs occurring in cabbage palm leaf bases, probably as a result of the relatively high moisture of this microhabitat (Swagel et al. 1997). *Ficus aurea* is native to the Caribbean Basin, with Florida representing the northern range limit (Serrato et al.

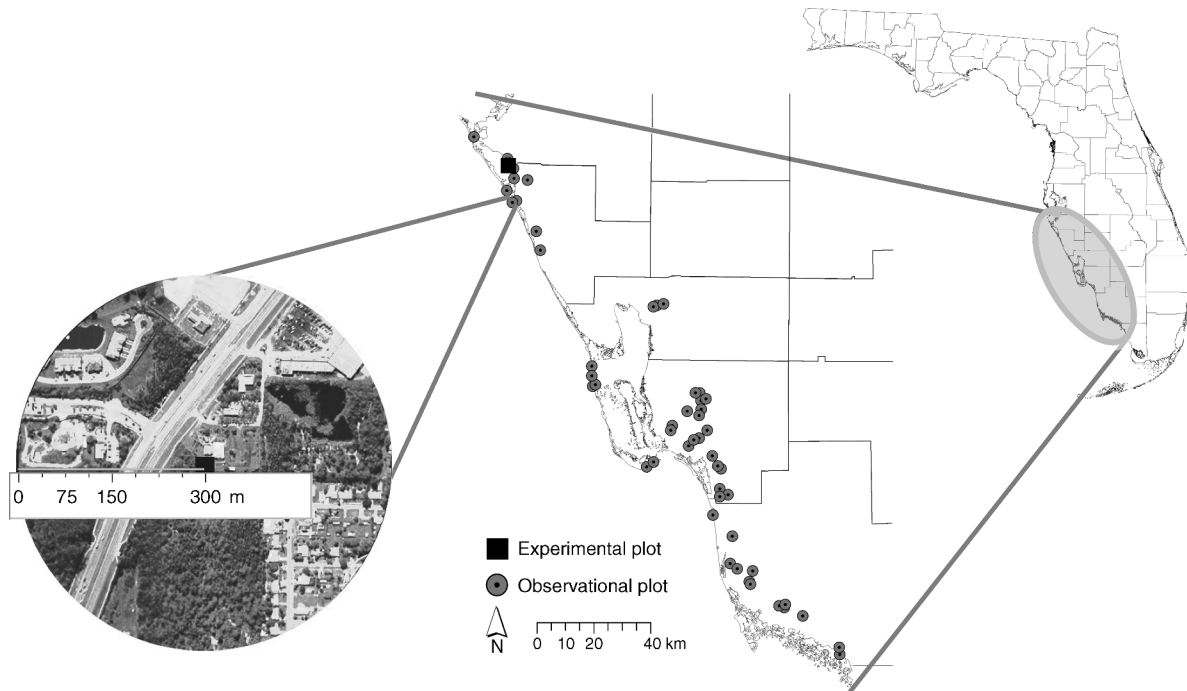


FIG. 1. Map of study region and scale of observational plots. From left to right: a single observational plot, the study region, and the state of Florida, USA. In the observational plots (see photo enlargement), abundance of juvenile strangler figs (native *Ficus aurea* and invasive *F. microcarpa*) was recorded in the  $30 \times 30$  m plot in the center (black square in the photo), and adult trees were recorded within 300 m of the juvenile plot. The experimental plot shown in the regional map (dark square) is the site at which the seed addition experiment was conducted. (The Satellite image is reproduced here courtesy of Google Earth Mapping Service.)

2004). *F. microcarpa* is native to South Asia and has become invasive around the world, including South America, Australia, and Pacific Islands (McPherson 1999, Corlett 2006). In Florida, *F. microcarpa* trees were deliberately planted as ornamental trees and have been present since at least 1912, but probably did not begin recruiting naturally until the fig's pollinator wasp species arrived around 1975 (Gordon 1998). The northernmost point in our study region was  $\sim 60$  km south of the zone where winter temperatures limit the range of *F. aurea*, which otherwise occurs throughout South Florida. In contrast, the current range boundary of *F. microcarpa* appears to be centered around human settlements on the coast of South Florida (EDDMaps 2011).

#### Study design

We quantified the distribution of fig trees in 52 plots, surveying each plot once between June 2006 and January 2009. Plots were distributed across the entire gradient of human disturbance, from downtown parking lots to native forest. Plot locations were selected using a stratified random approach to ensure equal representation of different habitats. Once a random location was selected, the  $30 \times 30$  m area with at least five cabbage palms nearest to the random point was used for the plot. All plots were located at least 1 km apart.

Each plot consisted of a  $30 \times 30$  m juvenile plot where all juvenile figs were counted, centered within a larger

circular adult plot with a radius of 300 m, where adult figs were surveyed (Fig. 1). We define a juvenile as a fig with dbh  $< 25$  cm (diameter at breast height), a reproductive threshold for *F. microcarpa* (T. Caughlin and J. H. Wheeler, unpublished data). When fig trees are large enough to be reproductive, they are generally rooted in the ground, so we were able to measure dbh from the ground. Within the juvenile plots, we recorded the number of cabbage palms  $> 2$  m tall, because an increased number of cabbage palms is likely to result in a higher chance of sampling juvenile fig trees. We also quantified canopy cover within the juvenile plots, because canopy cover alters light availability, a micro-habitat characteristic likely to affect fig establishment. We recorded canopy cover by visually estimating the amount of sky covered by vegetation  $> 2$  m high in five categories from 0–20% to 81–100% coverage. Canopy cover was recorded at 12 points, located every 5 m on two randomly selected parallel edges of the juvenile plot. We calculated the average value of these 12 points for use in analyses. Canopy cover was aggregated at the  $30 \times 30$  m scale, because this scale best reflects the overall differences between the wide range of habitats sampled by our juvenile plots.

The larger 300 m radius adult plot surrounding the juvenile plot was used to sample adult fig trees as potential seed sources. The total area of each of these adult plots is 28.27 ha, which is larger than the territories

TABLE 1. Data used to determine terms in Eq. 1 for habitat features, seed dispersal, and survival of strangler figs (native *Ficus aurea* and invasive *F. microcarpa*) in South Florida, USA.

Term in Eq. 1	Data used to represent term	Scale of data
Substrate	number of cabbage palms	30 × 30 m juvenile plots
Seed dispersal	distance to adult trees (Dist)	300 m radius centered around juvenile plot
	fig-eating bird habitat around adult trees (Adult.hab)	300 m radius centered around every adult tree
	presence/absence of adult trees (PA)	300 m radius centered around juvenile plot
Survival	canopy cover (CC)	30 × 30 m juvenile plots
	fig-eating bird habitat around center plot (Juv.hab)	300 m radius centered around juvenile plots

Note: Abbreviations in parentheses correspond to the terms in Table 2.

of most of the fig-eating birds in our study region (see Appendix A for more details). Because larger fig trees are likely to receive more frugivore visits (Korine et al. 2000), we assumed that larger trees would have a higher chance of dispersing seeds than smaller trees, and we sampled trees accordingly. Within 50 m of the juvenile plot, we recorded the location and dbh of all fig trees >25 cm dbh; within 100 m, we recorded all fig trees >50 cm dbh; within 200 m we recorded all fig trees >100 cm dbh; and within 300 m, we recorded all fig trees >200 cm dbh. The location of each fig tree and juvenile plot was measured with a Garmin 60Cxs GPS unit with 6-m accuracy (Garmin, Olathe, Kansas, USA). The 52 observational plots included a total area sampled of 4.68 ha for juvenile figs and 1470.27 ha for adult figs.

#### GIS data set and classification of favorable bird habitat

We created an index to describe habitat favorable to fig-eating birds by combining a satellite-derived land cover map with data on the abundance of fig-eating birds. We determined which resident bird species were potential fig seed dispersers by quantifying bird visitation rates to seven *F. aurea* and five *F. microcarpa* fruiting trees, during February–June 2006 (see Appendix A for details). The synconium (hereafter “fruit”) of both species is similar-sized (6–11 mm) and there were no significant differences in bird visitation between fig species (Appendix A). In total, 14 resident bird species were recorded visiting fig trees, with Northern Mockingbirds (*Mimus polyglottos*), Blue Jays (*Cyanocitta cristata*), and Red-Bellied Woodpeckers (*Melanerpes carolinus*) as the top three visitors, accounting for 38.7%, 20.8%, and 12.8% of visitation, respectively. We combined the bird visitation data with an independent set of bird abundance data (Stracey and Robinson, *in press*) to direct a classification of GIS land use data. These abundance data were collected in 2005 from auditory–visual counts of birds at 185 points across Florida. During each bird count, the surrounding habitat was visually classified (using categories similar to the land cover classification in the GIS data set; Appendix A: Table A2). We calculated the average number of “fig dispersers” per point for each habitat weighted by the percentage of visits of each bird species to fruiting fig trees, and used this value as an index of fig-eating bird habitat quality (see Appendix A for more details). Favorable habitat for fig-eating bird species

largely reflects human land use: high- and low-impact urban land cover classes had the highest values for fig-eating bird abundance (1.19 and 1.11, respectively), whereas the lowest value, 0.07, was found in pinelands habitat (Appendix A: Table A2).

We paired the bird data with Landsat Enhanced Thematic Mapper+ Satellite Imagery at 30 × 30 m resolution (Stys et al. 2004). This initial GIS data set with 28 habitat categories was reclassified into rasters representing fig-eating bird habitat quality. Next, we took a weighted average of all fig-eating bird habitat rasters within 300 m of every adult fig and juvenile plot. We assumed that effects of the landscape would decline with distance and calculated the weighted average of fig-eating bird habitat quality using the inverse distances between rasters and adult figs or juvenile plots as the weights.

#### Modeling juvenile abundance

Observed plant distributions represent a combination of seed dispersal and survival (Clark et al. 1999). We assumed that seed dispersal and survival were negative binomially and binomially distributed processes, respectively. Compounding these two distributions results in a negative binomial distribution for the number of juveniles in a 30 × 30 m plot (the response variable in all models), with expectation equal to expected seed rain multiplied by survival probability. We parameterized the negative binomial distribution with a mean,  $\mu$ , and a variance equal to  $\mu(1 + (\mu/k))$ , where the parameter  $k$  determines the degree of overdispersion. Our basic model structure is

$$\mu = \text{Substrate} \times \text{Seed dispersal} \times \text{Survival}. \quad (1)$$

The kinds of data used to represent each of these terms are shown in Table 1.

The substrate term is the number of cabbage palms in the 30 × 30 m plots. We assume that cabbage palm abundance affects the chances of sampling juvenile figs, rather than impacting seed dispersal or seedling survival. Thus, the number of cabbage palms in the model is included as a multiplicative term, independent of survival and seed dispersal.

The second term represents the seed dispersal process, considered here as

$$\text{Seed dispersal} = f + g \times \text{AT}. \quad (2)$$



Here,  $f$  is a parameter representing long-distance seed dispersal from beyond the 300 m radius plots where adult figs were surveyed. The term AT (adult trees) represents seed dispersal from trees within the 300 m radius plot and is weighted by the parameter  $g$ . We considered three different forms for AT. In the first form, AT is 0 or 1, respectively, for 300 m radius plots where no adults or at least one adult exceeded our distance-dependent dbh threshold. Hereafter, we refer to this first form of AT as “presence/absence” of adult trees, although we do not technically have presence/absence data because we did not perform a complete census of adult trees. In the presence/absence form of AT, expected seed rain is either  $f$  or  $f + g$ , respectively, for plots with or without at least one sampled adult. The second two forms were based on the following expression:

$$AT = f + g \sum_{i=1}^n \alpha_i / (dis_i + \gamma). \quad (3)$$

Here, AT includes a term for seed dispersal from individual adult trees  $i$  to the juvenile plot, summed over the  $n$  adult trees in the plot. In Eq. 3,  $dis_i$  is the distance from adult  $i$  to the plot center;  $f$  is the long-distance dispersal term;  $g$  and  $\gamma$  are fitted parameters; and  $\alpha_i$  is either 1 or  $adult.hab_i$  (the fig-eating bird habitat index in a radius 300 m around adult tree  $i$ ), depending on the version of the model. If seed arrival depends strongly on habitat quality for fig-eating birds in the surrounding landscape, then the model with  $\alpha_i = adult.hab_i$  should outperform the model with  $\alpha_i = 1$ . In preliminary analyses, we also considered models that accounted for the dbh of adult figs, as well as models based on alternative dispersal kernels (including lognormal and 2Dt kernels; Clark et al. 1999). These alternatives did not improve the fit to the data and are not considered further.

The third term in our model (Eq. 1) is

$$\begin{aligned} \text{Survival} = & \logit^{-1}(\beta_0 + \beta_1 \times \text{Canopy cover} \\ & + \beta_2 \times \text{Juvenile plot habitat}). \end{aligned} \quad (4)$$

This survival term consists of a parameter  $\beta_0$  representing baseline survival and two survival covariates, canopy cover and the fig-eating bird habitat index within a 300 m radius of the juvenile plot, with fitted parameters  $\beta_1$  and  $\beta_2$ . We do not include a temporal component for survival, because our seed addition experiment revealed that the vast majority (>99%) of mortality occurs during the first four months after seed dispersal, whereas annual survival for established seedlings is relatively high. We considered four possibilities for the covariates within the survival term: including both canopy cover and juvenile plot habitat ( $\beta_1$  and  $\beta_2$  both treated as free parameters); setting either  $\beta_1$  or  $\beta_2$  equal to zero so that only canopy cover or only juvenile plot habitat affects survival; and setting both  $\beta_1$  and  $\beta_2$  equal to zero,

indicating no effect of covariates. A consequence of this model structure is that canopy cover and fig-eating bird habitat around juvenile plots can affect juvenile fig abundance regardless of adult tree abundance within adult plots. If fig-eating bird habitat is correlated with unmeasured environmental variables that directly affect juvenile fig survival, models with fig-eating bird habitat around juvenile plots should fit better than models with fig-eating bird habitat around adult trees.

In total, we used combinations of the three seed arrival terms and the four survival terms to construct 10 models for each fig species. Models were fit in a maximum likelihood context in R version 2.10.1 (R Development Core Team 2010) using simulated annealing, a global optimization algorithm. High correlations (Pearson's  $r > 0.98$ ) between the survival parameter  $\beta_0$  and the seed dispersal parameters  $f$  and  $g$  resulted in extremely large confidence intervals. Removing  $\beta_0$  from the model (i.e., setting it to zero) did not significantly degrade the model's fit to data, whereas removing  $g$  or  $f$  significantly degraded the fit. Therefore, for the remainder of the paper we present results from models with  $\beta_0$  set to zero. Repeating the annealing algorithm several times with different initial conditions yielded very similar results, suggesting that the parameter estimates we obtained are close to the true maximum likelihood estimates. Model fit was evaluated using the small-sample version of Akaike's information criterion,  $AIC_c$ , (Burnham and Anderson 2002). We used  $R^2$  to evaluate the predictive capacity of each model by calculating the proportion of variance in  $\log(x + 1)$ -transformed juvenile fig abundance explained by each model (Lichstein et al. 2010). All analyses were conducted using R version 2.11.1 (R Development Core Team 2010).

#### Seed addition experiment

Because modeling observational data on plant distributions may confound seed dispersal and seedling establishment, we supplemented our observational data with a seed addition experiment. If seed arrival limits population growth rates, experimental seed addition should result in an increase in seedling abundance, whereas if establishment represents the main bottleneck for the population, adding seeds should not result in an increase in abundance (Clark et al. 2007). In May 2009, we added *F. microcarpa* and *F. aurea* seeds to cabbage palms in Sarasota, Florida (Fig. 1). We implemented the experiment at a site with a high abundance of *F. microcarpa* adults, where seed limitation was expected to be weak relative to other locations. Thus, the experiment constitutes a conservative test of seed limitation for *F. microcarpa*. We randomly selected 72 cabbage palms, embedded in an urban landscape with a variety of microhabitats, to serve as seed addition sites for each fig species. In each cabbage palm we placed five mesh pockets containing 0, 5, 10, 20, and 40 fig seeds, collected from at least six different individuals of each

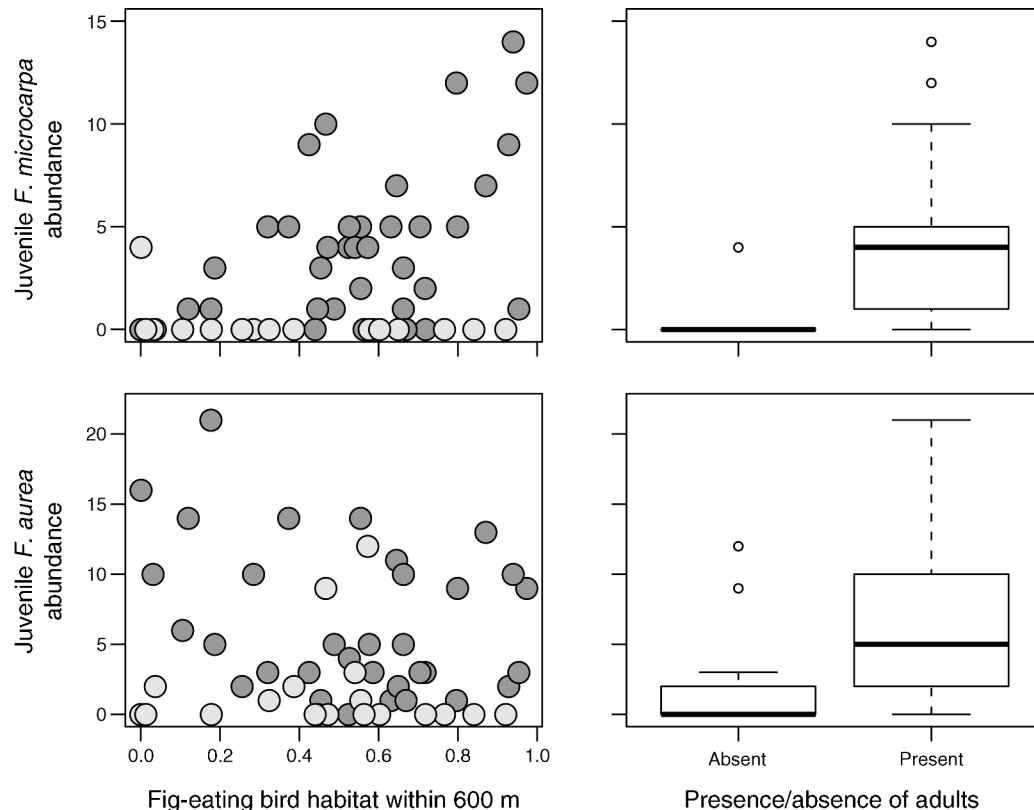


FIG. 2. Abundance of juvenile figs (*F. microcarpa* and *F. aurea*) plotted against favorable fig-eating bird habitat within 600 m of the juvenile plot (left-hand panels) and presence/absence of adult fig trees (right-hand panels). Favorable habitat is calculated as the average number of fig dispersers per point for each habitat, weighted by the percentage of visits of each bird species to fruiting fig trees. Dark gray and light gray circles indicate plots where adult conspecific figs were present and absent, respectively. The relationship between juvenile fig abundance and presence or absence of adult conspecific figs is shown in the box-and-whisker plots, where the black line represents the median, the horizontal lines on the box represent the first and third quartiles, the "whiskers" represent the maximum and minimum observations within 1.5 times the upper quartile, and the open circles represent outliers.

fig species in the study area, resulting in a total of 5400 seeds per species. Pockets were sewn closed on the bottom to prevent rain from displacing fig seeds, but were open at the top to allow naturally dispersed seeds to arrive in the pocket. Seeds were processed using the float method and a sieve to remove nonviable seeds. Germination rates of seeds processed using this technique were ~79% (A. Patel and D. Doan, *unpublished data*). Within each mesh pocket, we placed two tablespoons of humus collected from cabbage palm leaf bases, approximately equivalent to the amount naturally found in cabbage palm leaf bases. The number of seedlings in palms was recorded 4, 9, and 16 months after initial seed placement. We compared seedling establishment in treatments with zero seeds added to treatments with seeds added after the first census using a nonparametric Monte Carlo test, because zero seeds emerged from packets with zero seeds added. In a separate test, we used a logistic mixed model with survival of individual seeds as the response variable, fig species and number of seeds added as predictor variables, and nested random effects at the mesh pocket

and cabbage palm levels. The Monte Carlo analysis addresses the question of whether adding seeds increases seedling abundance, whereas the logistic mixed model analyzes survival effects on seeds that were added.

## RESULTS

### Summary statistics for juvenile and adult trees

Invasive fig adults were more closely associated with fig-eating bird habitat than were native fig adults: the index of fig-eating bird habitat quality within 300 m of *F. microcarpa* and *F. aurea* adults, respectively, was  $0.76 \pm 0.21$  and  $0.58 \pm 0.29$  (mean  $\pm$  SD), where habitat quality is measured as the average number of fig dispersers per point for each habitat weighted by the percentage of visits of each bird species to fruiting fig trees. In the 300 m radius circles around juvenile plots, the number of *F. aurea* adults was  $5.69 \pm 11.41$  individuals (mean  $\pm$  SD), compared to  $4.4 \pm 5.23$  *F. microcarpa* adults. *F. aurea* juvenile abundance in juvenile plots was higher ( $4.79 \pm 5.26$  individuals, mean  $\pm$  SD), than that of *F. microcarpa* ( $2.96 \pm 3.66$  individuals); see Fig. 2.

TABLE 2. Model selection results for *F. microcarpa* and *F. aurea*; each model contained both a seed dispersal and a survival term.

Model terms			<i>F. microcarpa</i>		<i>F. aurea</i>	
Seed dispersal	Survival	np	$\Delta\text{AIC}_c$	$R^2$	$\Delta\text{AIC}_c$	$R^2$
Adult.hab/Dist	CC	5	<b>0.00</b>	<b>0.73</b>	14.86	0.18
1/Dist	—	4	2.96	0.70	14.44	0.22
Adult.hab/Dist	—	4	3.34	0.69	12.43	0.21
1/Dist	Juv.hab + CC	6	5.37	0.7	11.46	0.32
1/Dist	—	4	8.45	0.65	13.05	0.17
1/Dist	Juv.hab	5	9.69	0.68	14.93	0.24
PA	CC	4	13.42	0.48	<b>0.00</b>	<b>0.43</b>
PA	Juv.hab + CC	5	14.99	0.55	2.63	0.43
PA	—	3	24.38	0.29	0.63	0.39
PA	Juv.hab	4	24.87	0.37	1.79	0.41

Notes: Abbreviations correspond to terms presented in Table 1. The “—” sign indicates an intercept-only survival term. Top-fitting models, in terms of  $\Delta\text{AIC}_c$ , for each species are shown in boldface. The total number of parameters (np) in each model is given.

#### Model fit and comparison

*F. microcarpa*.—The best model for juvenile *F. microcarpa* abundance included distance to adult trees, fig-eating bird habitat around adult trees, and canopy cover (Table 2). Both models incorporating fig-eating bird habitat into the dispersal term had  $\Delta\text{AIC}_c < 3.5$ , in contrast to the four models with fig-eating bird habitat in the survival term, which all had  $\Delta\text{AIC}_c > 5$ . Inverse models that did not include the distance-based dispersal term performed poorly: the best model without distance appeared in the model set with  $\Delta\text{AIC}_c = 13.42$ . The  $R^2$  values revealed a good fit to the data for *F. microcarpa*, with the model including distance, canopy cover, and fig-eating bird habitat around adult trees having the highest  $R^2$  value of 73%. Fig. 3 shows the relative strength of the two seed dispersal effects: distance to adult and fig-eating bird habitat quality around adults. Although the predicted number of juvenile figs declines exponentially with distance from adults, adult trees with a high fig-eating bird habitat index contribute more to juvenile abundance than trees with a low fig-eating bird habitat index, even at long distances.

*F. aurea*.—In contrast to the invasive *F. microcarpa*, the best-fit model for *F. aurea* included only presence/absence of adult trees within 300 m of juvenile plots and canopy cover (Table 2). The first model with a distance-based dispersal term had  $\Delta\text{AIC}_c = 11.46$ , indicating almost no empirical support for distance-dependent dispersal limitation. Predictive power of models for *F. aurea* was relatively low compared to that for *F. microcarpa*, with an  $R^2$  value of 43% for the best model. Parameter estimates and 95% confidence intervals for the best-fitting *F. microcarpa* and *F. aurea* models are presented as Tables B1 and B2 in Appendix B.

#### Seed addition experiment

In the first seedling census, four months after seed placement, 41 *F. aurea* and 20 *F. microcarpa* seedlings had established out of a total of 5400 seeds of each species added. However, after this initial four-month period, survival was relatively high, with 41% annual

survival for *F. aurea* and 70% annual survival for *F. microcarpa* seedlings. Zero seedlings emerged from pockets with zero seeds added, suggesting that few viable seeds were dispersed into the cabbage palm boots after experimental seed placement. Statistical tests were performed on seedlings from the first post-dispersal census in October 2009, because the number of seedlings was highest during this census, resulting in more statistical power to detect effects. There was a statistically significant difference in seedling emergence between pockets with seeds added and pockets with no seeds added ( $P = 0.036$ ; nonparametric Monte Carlo test). Comparing only pockets with seeds added, logistic mixed models of seedling survival showed no significant differences between fig species ( $P = 0.78$ ) or between different levels of seed addition ( $P = 0.82$ ).

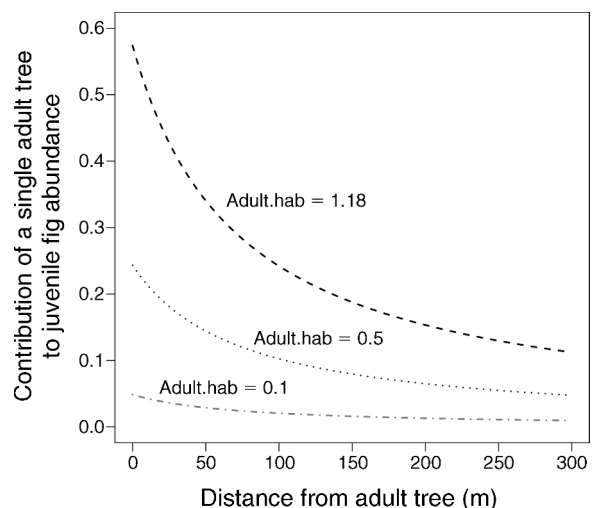


FIG. 3. Number of juvenile *F. microcarpa* in a sample plot predicted to originate from a single adult tree in the best-fitting model, as a function of distance from the sample plot to the adult. Each curve, indicated by “Adult.hab,” represents a different value of fig-eating bird habitat quality, spanning the range of values observed in the data.



PLATE 1. A juvenile *Ficus microcarpa* emerging from a cabbage palm leaf base. Photo credit: J. H. Wheeler.

#### DISCUSSION

Propagule pressure is increasingly recognized as a key process underlying invasion, and understanding how landscape context can alter dispersal distances and propagule availability is a research priority in invasion biology (Hastings et al. 2005). Two recent studies have suggested that microhabitat characteristics can amplify the impact of propagule pressure by increasing the number of favorable sites available for recruitment (Britton-Simmons and Abbott 2008, Eschtruth and Battles 2009). Our results support another possibility: at a large scale, landscape context could boost the effect of propagule pressure by increasing seed dispersal distances (With 2001). Our best models for the invasive fig species, *F. microcarpa*, support the hypothesis that juveniles are more abundant in landscapes with high human land use because of increased seed dispersal from fig-eating birds in urban habitats. However, our best models for the native fig species, *F. aurea*, did not include characteristics of individual adult trees, suggesting that effects of landscape context on seed dispersal may depend on the regional distribution of adult trees.

Determining whether environmental heterogeneity impacts invasive plant populations through seed or establishment limitation has consequences for invasive control strategies (Reaser et al. 2007). Although our analysis statistically partitions juvenile fig abundance into seed dispersal and survival components, we cannot make strong inferences about the relative importance of these two components solely from data on patterns of juvenile abundance. An ideal way to untangle factors related to seed limitation for invasive species would be a large-scale seed addition experiment over a range of habitats and seed availability (Denslow and DeWalt 2008). However, such an experiment with an invasive species would be logistically challenging and ethically questionable. Instead, we supplemented our large-scale observational study with a small-scale seed addition experiment. Our experiment revealed that natural recruitment of fig seedlings of both *F. aurea* and *F. microcarpa* is extremely rare, supporting the interpretation of our models that juvenile fig abundance largely reflects seed limitation.

We observed a positive correlation between invasive plant abundance and human land use, consistent with many previous studies (Burton et al. 2005, Bradley and



Mustard 2006, Seabloom et al. 2006). We allowed for effects of fig-eating bird habitat quality, reflective of human land use, in both the dispersal and the survival terms in our models of juvenile fig abundance. For *F. microcarpa*, models with fig-eating bird habitat around individual adult trees in the dispersal term fit better than models with fig-eating bird habitat around the juvenile plot in the survival term. These results are reflected in Fig. 2 (top left panel), which shows that an increase in fig-eating bird habitat results in increased juvenile *F. microcarpa* abundance only if adult trees are present. Examination of the parameterized dispersal term for *F. microcarpa* reveals that adult trees surrounded by little favorable bird habitat contribute almost nothing to juvenile abundance, even if the adult is close to the juvenile plot (Fig. 3).

Previous studies on wind-dispersed plants have shown that local neighborhood effects of tree density (Schurr et al. 2008) and spatial distribution of gaps (Bergelson et al. 1993) may change seed dispersal distances and ultimately rates of range expansion. In both of these studies, the scale used to examine the effects of environment on dispersal was less than 10 m. In comparison, when *F. microcarpa* adults are located in landscapes with high fig-eating bird habitat, our models suggest that even trees 300 m away from the juvenile plot have an effect on juvenile *F. microcarpa* abundance (Fig. 3). For animal-dispersed species, the scale at which landscape configuration affects dispersal may be much larger than for wind-dispersed species, highlighting the need to consider frugivory as a component of invasive plant spread (Buckley et al. 2006). A limitation of our study is that data on seed dispersal by the bird species that we observed eating figs, including quality of seed dispersal provided by each species, and daily movement patterns in different landscapes, were not available. More research on bird seed dispersal, including seed dispersal kernels for bird species that disperse invasive plants (e.g., Weir and Corlett 2007), could lead to more mechanistic models for invasive plant spread.

The best models predicting the abundance of juvenile *F. aurea* were very different than the best models for *F. microcarpa*. Instead of models incorporating favorable bird habitat and distance to adult trees, models with presence/absence of conspecific adults best predicted juvenile *F. aurea* abundance. The best models for *F. aurea* had relatively poor fits to the data, with the highest  $R^2$  values for predicted vs. observed values less than 40%, compared to 74% for the top *F. microcarpa* models. The relatively weak correlation between adult *F. aurea* trees and juveniles can also be observed in Fig. 2. Out of 16 plots with zero adult *F. microcarpa* within 300 m, only one plot contained a single *F. microcarpa* juvenile, whereas out of 18 plots with zero *F. aurea* adults, seven contained *F. aurea* juveniles. How can these results be reconciled with our seed addition experiment, which showed no significant differences in seed limitation between *F. aurea* and *F. microcarpa*?

Seed limitation is a combination of multiple factors, including tree fecundity, the density and dispersion of seed sources, and seed dispersal (Clark et al. 1998). For *F. microcarpa*, an invasive plant at the edge of its rapidly expanding range, distance to individual seed sources, which are comparatively few, may be crucial for juvenile abundance. For *F. aurea*, with a more uniform density of adult trees within an established range, seed arrival into cabbage palms may still be limited by the overall fecundity and density of adult trees, but less limited by distance to any single individual tree. These results highlight the potential complexities underlying the concept of seed limitation. Although seed addition experiments are a useful tool for quantifying the degree of seed limitation, observational data may still be valuable for determining whether seed limitation is a result of adult tree density, fecundity, or seed dispersal.

Range expansion of many invasive plants requires seed dispersal by animals, which are likely to deposit most seeds <1 km from the parent plant (Clark et al. 1999). Yet, invasive plant range expansion also entails distributional shifts at much larger scales as populations move from the locus of introduction, often an urban area, into other landscapes. Ultimately, quantifying the relationship between landscape context and seed dispersal could lead to better techniques for controlling invasive species. Our study suggests that the most effective strategy to reduce invasive fig recruitment would be to remove *F. microcarpa* adult trees located in landscapes with a high amount of fig-eating bird habitat, rather than targeting all adult trees equally or restricting human land use regardless of adult tree abundance.

#### ACKNOWLEDGMENTS

Thanks to D. R. Gordon, K. Kitajima, M. D., Lowman, E. M. Bruna, D. J. Levey, F. E. Putz, J. R. Poulsen, G. A. Gale, and K. Sauby for comments on the manuscript. C. M. Stracey and S. K. Robinson shared the bird abundance data. This research was funded by a FLEPPC Student Research Grant and the National Science Foundation under Grant No. 0801544 in the Quantitative Spatial Ecology, Evolution and Environment Program at the University of Florida.

#### LITERATURE CITED

- Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rates of weed spread in spatially heterogeneous environments. *Ecology* 74:999–1011.
- Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications* 16:1132–1147.
- Britton-Simmons, K. H., and K. C. Abbott. 2008. Short- and long-term effects of disturbance and propagule pressure on a biological invasion. *Journal of Ecology* 96:68–77.
- Buckley, Y. M., et al. 2006. Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology* 43:848–857.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Burton, M. L., L. J. Samuelson, and S. Pan. 2005. Riparian woody plant diversity and forest structure along an urban–rural gradient. *Urban Ecosystems* 8:93–106.

- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170:128–142.
- Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68:213–235.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. H. Lambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8:1023–1037.
- Condit, R., et al. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.
- Corlett, R. T. 2006. Figs (*Ficus*, Moraceae) in urban Hong Kong, South China. *Biotropica* 38:116–121.
- Denslow, J. S., and S. J. DeWalt. 2008. Exotic plant invasions in tropical forests: patterns and hypotheses. Pages 409–426 in W. P. Carson and S. A. Schnitzer, editors. *Tropical forest community ecology*. Wiley-Blackwell, Chichester, UK.
- EDDMapS. 2011. Early detection and distribution mapping system. University of Georgia, Center for Invasive Species and Ecosystem Health, Tifton, Georgia, USA. <http://www.eddmaps.org/> [Accessed 3 June 2011.]
- Eschtruth, A. K., and J. J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs* 79:265–280.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8:975–989.
- Hastings, A. K. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8:91–101.
- Korine, C., E. K. V. Kalko, and E. A. Herre. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123:560–568.
- Leishman, M. R., and V. P. Thomson. 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *Journal of Ecology* 93:38–49.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics* 34:549–574.
- Lichstein, J. W., J. Dushoff, K. Ogle, A. Chen, D. W. Purves, J. P. Caspersen, and S. W. Pacala. 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. *Ecological Applications* 20:684–699.
- McPherson, J. R. 1999. Studies in urban ecology: strangler figs in the urban parklands of Brisbane, Queensland, Australia. *Australian Geographical Studies* 37:214–229.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- Reaser, J. K., L. A. Meyerson, and B. Von Holle. 2007. Saving camels from straws: how propagule pressure-based prevention policies can reduce the risk of biological invasion. *Biological Invasions* 10:1085–1098.
- Schurr, F. M., O. Steinitz, and R. Nathan. 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology* 96:628–641.
- Seabloom, E. W., J. W. Williams, D. Slayback, D. M. Stoms, J. H. Viers, and A. P. Dobson. 2006. Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications* 16:1338–1350.
- Serrato, A., G. Ibarra-Manríquez, and K. Oyama. 2004. Biogeography and conservation of the genus *Ficus* (Moraceae) in Mexico. *Journal of Biogeography* 31:475–485.
- Simberloff, D. 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 40:81.
- Stracey, C. M., and S. K. Robinson. *In press*. Does nest predation shape urban bird communities? *Studies in Avian Biology*.
- Stys, B., R. Kautz, D. Reed, M. Kertis, R. Kawula, C. Keller, and A. Davis. 2004. Florida vegetation and land cover data derived from 2003 Landsat ETM+ imagery. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA.
- Swagel, E. N., A. V. H. Bernhard, and G. S. Ellmore. 1997. Substrate water potential constraints on germination of the strangler fig *Ficus aurea* (Moraceae). *American Journal of Botany* 84:716.
- Uriarte, M., M. Anciães, M. T. B. da Silva, P. Rubim, E. Johnson, and E. M. Bruna. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecology* 92:924–937.
- Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218.
- Weir, J. E. S., and R. T. Corlett. 2007. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology* 22:131–140.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conservation Biology* 16:1192–1203.

## SUPPLEMENTAL MATERIAL

### Appendix A

Additional methods and results for deriving fig-eating bird habitat quality index (*Ecological Archives* E093-140-A1).

### Appendix B

Parameter estimates and 95% confidence intervals for best-fitting models of juvenile fig abundance (*Ecological Archives* E093-140-A2).