Reproductive failure of a long-lived wetland tree in urban lands and managed forests

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Summary

1. Land use (e.g. urbanization, agriculture, natural lands management) may directly affect populations by habitat loss and fragmentation, and indirectly by altering conditions needed for reproductive success. The effects of urbanization are especially pronounced for populations that remain among urbanized areas, but they are difficult to detect in long-lived species.

2. We evaluated the effects of urbanization on the recruitment of cypress (*Taxodium distichum*), a long-lived coniferous tree that dominates isolated wetlands in Orlando, Florida, USA, a rapidly urbanizing region. Cypress requires saturated but not flooded soils to germinate, and seedlings are easily out-competed in the absence of fire. We hypothesized that urbanization has altered the hydrology and fire regimes, leading to biological inertia and reduced cypress recruitment relative to managed forest and ranchland.

3. We found low cypress recruitment in urban areas, but surprisingly in managed forest as well. Many cypress populations in managed forest were bounded by fire breaks which prevent upland fires from burning into the wetlands. Ranchland had significantly more recruitment than urban and managed forest, and these wetlands did not have fire breaks.

4. In urban lands, the effects of urbanization were delayed. Cypress recruitment initially occurred near the edge of wetlands where hydrological conditions were most favourable, but virtually stopped at 20 years post-urbanization. Cypress recruitment also occurred near the edge of the wetlands in managed forests and ranchlands and was higher in larger wetlands.

5. *Synthesis and applications*. Urbanization is associated with the eventual reproductive failure of cypress and in the absence of management practice changes, cypress recruitment may cease in many additional wetlands. If past urbanization rates continue, 80–90% of cypress populations in isolated wetlands in the path of urban sprawl could permanently cease recruitment in 100 years. Reducing urban sprawl and introducing prescribed fire in managed-forest cypress domes could mitigate this effect and conserve reproduction of this long-lived, dominant tree species and the diversity of the wetlands they typify.

Key-words: biological inertia, cypress dome, fire, Florida, forest management, hydrology, isolated wetlands, recruitment, south-eastern US, urbanization

Introduction

Conversion of land to urban use (urbanization) is one of the leading causes of native species diversity loss because it directly and indirectly reduces or exterminates some populations. Human population growth in urban areas is increasing at rapid rates (UNFPA 2007) and nearly 84% of the US population is now living in metropolitan areas (U.S. Census Bureau 2000, 2010). As a result of this rapid and global pattern of landscape change, it is important to understand the direct and indirect effects of urbanization on natural populations (Valdés & García 2011).

Relatively obvious, direct effects of urbanization include permanent destruction and fragmentation of natural habitats (McKinney 2002; McDonald, Kareiva & Forman 2008). Direct effects vary widely among cities and regions and can be assessed at large scales with remotely sensed data (Jantz, Goetz & Jantz 2005; Dewan & Yamaguchi 2009; Ranta & Viljanen 2011). More subtle, indirect effects of urbanization include recruitment failure and genetic effects as a result of habitat degradation and

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fragmentation (Matthies *et al.* 2004; Kolb 2005) and they may be especially difficult to detect in long-lived species (Colling, Matthies & Reckinger 2002).

Natural populations of long-lived species may initially seem to resist the biological changes that occur with urbanization because the established individuals remain within urban areas. However, these populations may be exhibiting 'biological inertia' where populations temporarily persist despite unfavourable conditions (Gorham 1957; Summerfield 1972; Harper & White 1974; VonHolle, Delcourt & Simberloff 2003). Biological inertia was initially used to describe early successional plants that remain in later successional stages but the remaining adult plants no longer recruit, temporarily preventing full succession (Gorham 1957; Summerfield 1972; Harper & White 1974). Native plant populations can also display biological inertia when resident adults remain in unfavourable conditions, preventing invasion of introduced species (VonHolle, Delcourt & Simberloff 2003). Here, we apply the term to describe long-lived species that remain as adults in areas with local habitat degradation (i.e. from land-use alterations) but are no longer reproducing, temporarily preventing detection of the habitat degradation. However, the ultimate success of populations depends on recruitment success (Ranta, Tesar & Kaitala 2002), and so even dominant, long-lived species may be sensitive to land-use change if it strongly affects juvenile life stages. In addition, widespread habitat degradation (e.g. urbanization) could cause multiple populations to exhibit biological inertia and lead to an extinction debt for that species in those habitats (Tilman *et al.* 1994; Vellend *et al.* 2006).

Freshwater wetlands and populations of long-lived species (e.g. trees) that inhabit wetlands can remain among areas undergoing urbanization because they may be legally protected or difficult to drain or fill. As a result, some wetlands may be destroyed during urbanization but others remain and wetland populations can continue. Such remaining populations provide an opportunity to test for subtle indirect effects of urbanization, with results that have meaning for conservation of the species and their wetland habitats.

Here we report land-use effects on recruitment of a coniferous tree, cypress (*Taxodium distichum*), which dominates the numerous forested wetlands of the southeastern United States (a rapidly urbanizing region) and can live for centuries, like its redwood and sequoia relatives. Two varieties of cypress have been recognized, baldcypress and pondcypress, but little genetic differences have been found (Tsumura *et al.* 1999; Lickey & Walker 2002). We often found both morphologies in the same wetland and even on the same individual, thus, we do not distinguish between the two varieties and refer to *T. distichum* in this study as cypress. Isolated (non-riverine) wetlands dominated by cypress are called 'cypress domes' because trees are naturally taller in the middle and shorter around the edge.

Cypress has specific germination requirements that we hypothesize should be negatively affected by urbanization. Cypress requires saturated but not flooded soils to germinate, and seedlings must remain above the water level for the first year to survive (Brandt & Ewel 1989; Burns & Honkala 1990). However, cypress domes remaining among urbanized areas are often used in stormwater systems as retention ponds and receive runoff to avoid flooding roads and buildings; cypress domes then remain flooded beyond cypress seedling requirements. Alternatively, cypress domes may be drained during urbanization to reduce flooding risk. We hypothesized that this 'polarization' of wetland hydrology alters the naturally variable hydrology of cypress domes, likely affects cypress recruitment, and contributes to biological inertia in this long-lived species.

Management and urbanization also change the fire regimes in which many species have evolved. Florida includes naturally pyrogenic landscapes, in which fire is required to maintain many native ecosystems, (Mitchell *et al.* 2006; Slapcinsky, Gordon & Menges 2010) including cypress domes (Penfound 1952; Marois & Ewel 1983; Casey & Ewel 2006). Fires are actively suppressed in urban areas, but fire suppression in cypress domes allows for encroachment of other woody vegetation that may out-compete or shade out cypress seedlings (Ewel 1995). Thus, changes to fire regime with urbanization should also contribute to biological inertia in cypress populations.

Alterations to fire and hydrology regimes are difficult to measure directly. Record keeping for occurrence and extent of prescribed fires or wildfires on private lands is nearly non-existent and pre-urban fire regime is unknown. Hydrological alterations to any urban wetland are difficult to quantify because stormwater systems are extensive and pre-urban hydrology cannot be interpreted. The alterations to fire and hydrological regimes that occur during urbanization are known (Sharitz *et al.* 1992; Russell, Van Lear & Guynn 1999; Ehrenfeld 2000; Faulkner 2004; Kentula, Gwin & Pierson 2004), and both alterations are important factors influencing cypress populations (Penfound 1952; Brandt & Ewel 1989; Burns & Honkala 1990; Casey & Ewel 2006). Thus, quantifying urbanization surrounding cypress domes can serve as a proxy to directly measuring changes in hydrological and fire regimes without the risks associated with experimental application of those regimes in urban areas.

Cypress domes also provide three practical advantages to study biological inertia as a result of land-use change: (i) cypress trees are easily distinguished on colour-infrared photographs (McCauley, Jenkins & Quintana-Ascencio 2012), making it possible to evaluate habitat degradation and loss across large spatial scales and through decades; (ii) urbanization of cypress domes occurs rapidly relative to the life span of cypress trees, meaning that adult and juvenile trees provide an approximate before and after urbanization comparison; and (iii) geographically separate cypress domes provide a naturally replicated system to

test for general patterns across an urbanization gradient; we specifically excluded riverine cypress populations from the study.

We hypothesized that urbanization would reduce cypress recruitment and predicted that recruitment would decrease along an urbanization gradient (i.e. wetlands embedded in managed forest, ranchland and urban landscapes). We also sought to determine the factors that most affect cypress recruitment in cypress domes of urban areas, managed forests and ranchlands and to predict future cypress recruitment in the region.

Materials and methods

STUDY AREA

The study was conducted in Orange and Seminole counties in the Orlando region of central Florida USA (28°36′N, 81°18′W; *c*. 350 000 ha). The Orlando metropolitan region is typical of recent population growth in the south-eastern United States and has thousands of cypress domes that remain among the current urbanized areas (McCauley, Jenkins & Quintana-Ascencio 2012).

IDENTIFYING CYPRESS DOMES

Colour-infrared aerial photographs and land cover data from 2004 were obtained from the St. Johns River Water Management District for the study area. Using ArcGIS 9.2 (ESRI 2006), polygons identified as forested wetlands in the land cover data were extracted and overlaid on top of the colour-infrared aerial photography. At a 1 : 12 000 scale, the entire study area was scanned and the wetlands in the forested wetlands data layer were removed, added and modified as necessary to create an accurate layer of cypress domes. Cypress is readily distinguishable on colour-infrared aerial photography making cypress domes easy to visualize (McCauley, Jenkins & Quintana-Ascencio 2012). This manual processing technique was more accurate than automated techniques, as verified by subsequent field studies. Cypress wetlands that were in close proximity to riverine habitats were removed to obtain a data layer of 'isolated' cypress domes.

DETERMINING URBANIZATION GRADIENT

We categorized land cover surrounding each cypress dome to quantify urbanization intensity. We first created a buffer in Arc-GIS v.9.2 (ESRI, 2006) around each cypress dome equal to the average nearest-neighbour distance (263 m). Based on descriptions provided with the land cover data layer, five potential land cover categories were identified: managed forest, ranchland, low-intensity urban, medium-intensity urban or high-intensity urban. For example, land cover descriptions such as golf courses, recreation and low-density housing were classified as low-intensity urban and descriptions such as cattle operations, crops and citrus groves were classified as agricultural (identified here as ranchlands because those strongly dominated). Principal Component Analysis (PCA) was used to ordinate the locations characterized by the proportions of each of the five land cover categories within the buffer and obtained two multivariate axes. Each axis

was plotted against each of the five original land cover proportions. Each graph was evaluated and a range of axis values that represented that category was estimated, based on where the majority of points fell on the graph. For example, when each axis was plotted against the agricultural proportions in each buffer, the majority of points that were high in agriculture were less than −0·5 for axis 1 and between −1 and 1 on axis 2. The ranges obtained from the graphs were used to assign each cypress dome into one of the five categories (Fig. 1). Canonical Discriminant Analysis was used to test the categories, and 92·4% of the cases were classified correctly, which we considered sufficient to represent the urbanization gradient.

FIELD DATA COLLECTION

Sixteen cypress domes were randomly selected from each land cover category for sampling and were divided equally between small (<0·5 ha) and large (>0·5 ha) cypress domes. Several, random, 100-m^2 plots, covering 2% of the area of each cypress dome, were generated, with a minimum of two plots per cypress dome. Preliminary analysis compared cypress density data obtained from random plots that covered 1%, 2%, 3% and 5% of dome area and no significant difference was found between percentages. We sampled plots to equal 2% of the area of the dome to obtain sufficient sample size. Preliminary analysis of 1762 cypress trees also found that no trees ≤2 m height had cones, but trees >2 m could have cones. We identified any tree <2 m height as a juvenile, and trees >2 m height were considered adults. Within each plot, the number of adults and the number of juveniles were recorded.

A subcanopy index was also recorded for each plot; this comprised a digital equivalent of cover board methods to evaluate subcanopy vegetation thickness, which should reduce cypress recruitment (Griffith & Youtie 1988; Holway 1991; Connell, Lowman & Noble 1997; Rosell, Patch & Salmons 2007). A digital picture was taken, of a 0·9 m × 1·5 m piece of blue vinyl, displayed vertically, at a height of 2 m and at a distance of 10 m in the plot. Measuring Vegetation Health Analysing Digital Images software (Pickle & Kirtley 2004) was used to quantify the area of
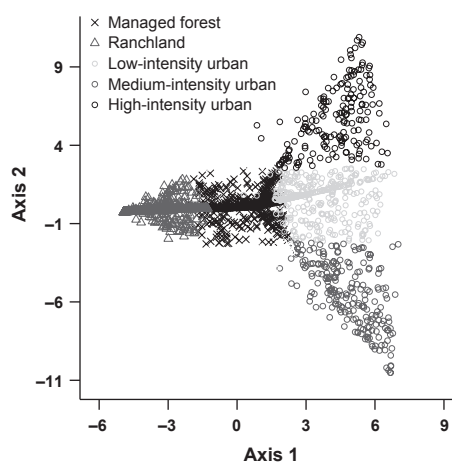

Fig. 1. Principal component analysis (PCA) results. PCA Axis 1 separates managed-forest, ranchland and urban domes, whereas PCA Axis 2 separates low-intensity, medium-intensity and high-intensity urban cypress domes.

blue visible through the vegetation. The subcanopy index was calculated as 1−(visible blue area/total blue area). Two such index values were obtained at each plot and averaged. Subcanopy index values ranged from 0 to 1, with 1 being the greatest amount of subcanopy vegetation present.

GIS VARIABLES

Using ArcGIS (ESRI 9.2, 2006), *a posteriori* variables were calculated including distance from the plot to the wetland edge as the proportion of the wetland radius [distance from the plot to the edge of the wetland/(distance from the plot to the edge of the wetland + distance from the plot to the centre of the wetland)]. For urban-categorized cypress domes, time since urbanization was calculated from Orange and Seminole County property parcel databases (managed-forest and ranchland cypress domes had no time since urbanization). Cypress dome area was also calculated in GIS and used as a predictor variable in additional analyses.

DIFFERENCES IN RECRUITMENT AMONG LAND COVER CATEGORIES

Recruitment was analysed as both the number of juveniles and the ratio of juveniles to adults. The number of juveniles was compared among land cover categories using a zero-inflated Poisson regression model (PSCL package; Zeileis, Kleiber & Jackman 2008) in R (R Development Core Team 2011), with distance to edge of wetland as a covariate. A chi-squared test on the difference of log likelihoods was used to determine whether this model was significantly better than the null model (Zeileis & Hothorn 2002). A Vuong test was used to evaluate if the zero-inflated Poisson regression model was significantly better than a simple Poisson model (Vuong 1989). This procedure was repeated with different grouping variables to test for significant differences in (i) non-urban (i.e. managed forest and ranchland) vs. urban cypress domes and (ii) ranchland cypress domes vs. all other land cover categories.

The juvenile-to-adult ratio was also used as a response variable because it normalized the number of juveniles to the adult population size, but a substantial number of zeros prevented transformations to meet normality or variance assumptions of traditional ANOVA analyses. Instead, we used Monte Carlo simulation tests (1000 permutations) in R v.2.13.0 (R Development Core Team 2011) to test for significant differences in juvenile-to-adult ratios among land cover categories because parametric assumptions were not made.

FACTORS AFFECTING RECRUITMENT IN URBAN CYPRESS DOMES

Recruitment was expected to vary among wetlands and among sample locations within wetlands. We used mixed-effects models to analyse variation among wetlands as a random effect and variation of covariates within wetlands as fixed effects. Mixed-effects models were analysed in R v2.13.0 (R Development Core Team 2011) using the LME4 package (Bates, Maechler & Bolker 2011).

In urban cypress domes, we evaluated the association between predictor variables and the presence or absence of juveniles using a model selection approach. The predictor variables in the logistic regression models compared various combinations of distance to the edge of the wetland, cypress dome area, subcanopy index, time since urbanization and different levels of urbanization (PCA Axis 2; Fig. 1). We selected the most informative model as the one having the lowest Akaike's Information Criterion (AIC; Akaike 1973; Burnham & Anderson 2001) value and highest weight. Model weights indicate the likelihood of each model in comparison with the other models. Thirty total models were compared to determine the best predictors for juvenile presence in urban cypress domes. Relative variable importance values were also calculated by adding the weights of each model in which a particular variable appeared; they were calculated using all 30 models.

FACTORS AFFECTING RECRUITMENT IN MANAGED-FOREST AND RANCHLAND CYPRESS DOMES

In managed-forest and ranchland cypress domes, the juvenile-to-adult ratio (log transformed) was used as a response variable in linear mixed-effects regressions. Predictor variables were distance to the edge of the wetland, area of cypress dome, subcanopy index and PCA Axis 1. Linear mixed-effects models produced by the lme4 package (Bates, Maechler & Bolker 2011) do not report *P*-values so we conducted Markov chain Monte Carlo simulations with 10 000 permutations and calculated *P*-values from outcomes based on the *t*-statistic with the upper bound for the degrees of freedom (Baayen 2011). We selected the most informative model as above. Fifteen total models were run to determine the best predictors for juvenile-to-adult ratio in managed-forest and ranchland cypress domes. Relative variable importance values were calculated using all 15 models.

PROJECTION TO OTHER CYPRESS DOMES IN SPACE AND TIME

We used the parameters from the most informative mixed-effects regression models to simulate estimates of cypress recruitment in non-sampled cypress domes in 2004. We simulated 100 iterations of the model for each wetland dome to evaluate the random (wetland dome) and fixed effects (i.e. distance to the edge, cypress dome area, etc.). The 100 fitted values were then averaged to obtain one robust value of probability of juvenile presence (for urban cypress domes) and juvenile-to-adult ratio (for managed-forest and ranchland cypress domes). The regression fitted values were used to create maps in ArcGIS version 9.2 (ESRI 2006).

The recruitment projection values were combined with estimates of wetland loss (McCauley, Jenkins & Quintana-Ascencio 2012) to project total cypress domes remaining and total cypress domes recruiting in 100 years. Destruction and degradation caused a 20% loss of cypress domes and the conversion of 26% of the managed-forest cypress domes to urban categories over a 20-year period (McCauley, Jenkins & Quintana-Ascencio 2012). During the same time period, 26% of the ranchland cypress domes were lost and 3% were converted to urban categories (McCauley, Jenkins & Quintana-Ascencio 2012). Recruitment in managed-forest and ranchland domes were analysed as a juvenile-to-adult ratio and those domes with a ratio of <0·5 were categorized as having recruitment absent. Recruitment in urban cypress domes were analysed as a binary variable, absent or present.

Results

DIFFERENCES IN RECRUITMENT AMONG LAND COVER CATEGORIES

A simple urbanization gradient (from managed forest to ranchland to low-intensity, medium-intensity, and high-intensity urban) did not correspond to cypress recruitment. Instead, ranchland cypress domes had higher recruitment than other categories, and managed-forest cypress domes recruited no better than urban cypress domes (Fig. 2). Land-use category, with distance to the edge as a covariate, significantly predicted the number of juveniles using the zero-inflated Poisson regression model ($P = 0.02$), which was significant compared to the null model ($\chi^2 = 30.85$, d.f. = 4, $P < 0.0001$) and a significant improvement over a standard Poisson model (Vuong test; $P < 0.0001$). Surprisingly, our data did not detect differences in number of juveniles among land-use categories when managed-forest and ranchland cypress domes were grouped together and compared to urban cypress domes grouped together ($P = 0.0994$). However, ranchland cypress domes had significantly more juveniles than all other land-use categories combined ($P < 0.0001$). Monte Carlo simulations also showed significantly different juvenile-to-adult ratio among the land-use categories ($P < 0.0001$).

FACTORS AFFECTING RECRUITMENT IN URBAN CYPRESS DOMES

Time since urbanization ($z = -2.22$, $P = 0.026$) and distance to the edge of the wetland ($z = -2.51$, $P = 0.01$) best explained the juvenile-to-adult ratio in urban cypress domes (Table 1, Fig. 3). Using a presence/absence
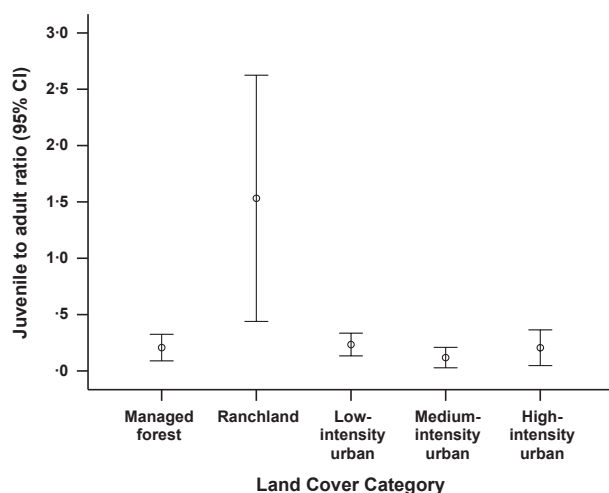
Table 1. Top five models for predicting probability of juvenile presence in urban cypress domes in central Florida. Thirty total models were run but only the top five models are shown*

Model	AIC	Δ_i	log (£)	w_i
Distance to edge + time since urbanization	150·10	0·000	1·000	0·425
Subcanopy index + distance to edge + time since urbanization	151·70	1·600	0·449	0·191
PCA axis 2 + distance to edge + time since urbanization	152·00	1·900	0·387	0·164
Subcanopy index + PCA axis 2 + distance to edge + time since urbanization	153·40	3·300	0·192	0·082
Time since urbanization	154·30	4·200	0·122	0·052

AIC, Akaike Information Criterion value (lower values indicate better models); log (£), log likelihood; Δ_i, difference between lowest AIC value and AIC_i; w_i, model weight; PCA, principal component analysis.
*Relative variable importance of all models: time since urbanization: 0·988, distance to edge: 0·893, PCA Axis 2: 0·287, subcanopy index: 0·037, area of cypress dome: 0·028.
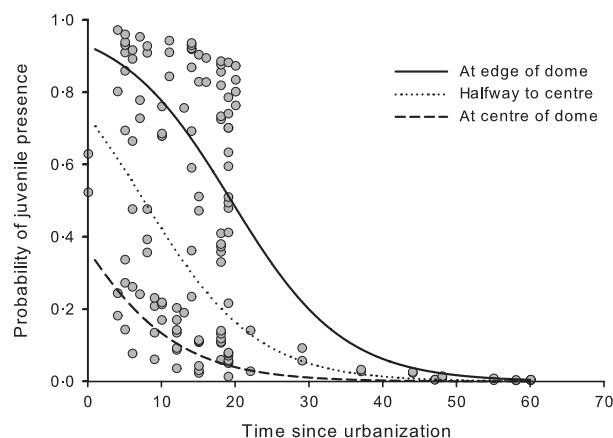

Fig. 3. Mixed-effects logistic regression model with fitted values of the sampled domes. Juvenile-to-adult ratio drops significantly around 20 years post-urbanization and is higher at the edge of the dome than in the centre.

threshold of 0·5 (as in a binomial coin toss), this model correctly evaluated 94% of absences and 93% of presences. Less cypress recruitment occurred in the centre of cypress domes than on the edges, and recruitment dropped precipitously at about 20 years after urbanization (Fig. 3). Consistent with that model, no recruitment was observed in any sampled cypress dome that had been urbanized for more than 22 years (Fig. 3). In decreasing order, the relative variable importance of model variables were as follows: time since urbanization (0·988), distance to the edge of the wetland (0·893), Axis 2 (0·287, associated with level of urbanization), subcanopy index (0·037) and area of cypress dome (0·028).

Fig. 2. Juvenile-to-adult ratios among the five land cover categories. Ranchland cypress domes had a significantly higher juvenile-to-adult ratio than other land cover categories. Managed-forest and urban cypress domes did not have a significantly different juvenile-to-adult ratio.

FACTORS AFFECTING RECRUITMENT IN MANAGED-FOREST AND RANCHLAND CYPRESS DOMES

The greatest cypress recruitment occurred on the edge of large, ranchland cypress domes, rather than in cypress domes in managed forests. The most informative model (Table 2) was the model with PCA Axis 1 ($P_{MCMC} = 0.066$, $t = -1.92$, $P_t = 0.080$; associated with the gradient between managed-forest, ranchland and urban domes), distance to the edge of the wetland ($P_{MCMC} = 0.030$, $t = -2.71$, $P_t = 0.005$) and area of the cypress dome ($P_{MCMC} = 0.0001$, $t = 3.691$, $P_t < 0.0001$). A verification of model fit to the data using a linear regression of predicted vs. observed values yielded an R^2 of 0.764. Juvenile-to-adult ratio was negatively correlated with PCA Axis 1 and distance to the edge of the wetland and positively correlated with cypress dome area (Fig. 4; lower Axis 1 values correspond to ranchland cypress domes – see Fig. 1). In decreasing order, the relative variable importance of model variables was as follows: area of cypress dome (0.986), distance to the edge of the wetland (0.881), PCA Axis 1 (0.656) and subcanopy index (0.267).

PROJECTION TO OTHER CYPRESS DOMES IN SPACE AND TIME

Using a presence/absence threshold of 0.5, only 114 of 728 urban cypress domes (15.7%) were estimated to be recruiting cypress in 2004 and those cypress domes typically fall on the periphery of urbanized areas (Fig. 5). In addition, juvenile-to-adult ratios in low- and high-recruiting cypress domes of managed forest and ranchland in 2004 were spatially intermixed, with the highest recruitment projected to occur in the largest cypress domes.

We project that very few cypress dome populations within urban areas and managed forest will continue to

Table 2. Top five models for predicting juvenile-to-adult ration in managed-forest and ranchland cypress domes in central Florida. Fifteen total models were run but only the top five models are shown*

Model	AIC	Δ_i	log (£)	w_i
PCA axis 1 + distance to the edge + dome area	−33.64	0	1	0.42
Distance to the edge + dome area	−32.11	1.53	0.47	0.20
PCA axis 1 + subcanopy index + distance to the edge + dome area	−31.66	1.98	0.37	0.16
Subcanopy index + distance to the edge + dome area	−30.48	3.16	0.21	0.09
PCA axis 1 + dome area	−29.25	4.39	0.11	0.05

AIC, Akaike Information Criterion value (lower values indicate better models); log (£), log likelihood; Δ_i, difference between lowest AIC value and AIC_i; w_i, model weight; PCA, principal component analysis.
*Relative variable importance of all models: dome area: 0.986, distance to edge: 0.881, PCA axis 1: 0.656, subcanopy index: 0.267.
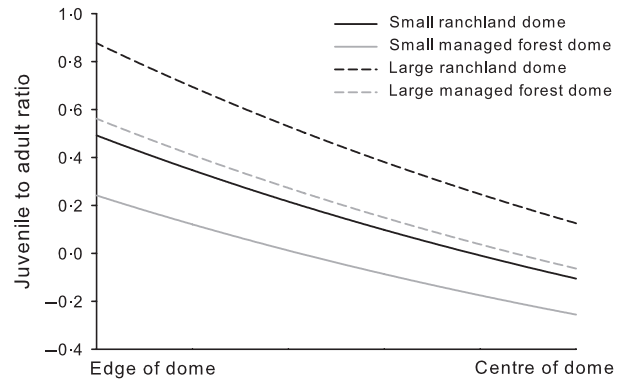

Fig. 4. Mixed-effects linear regression model of juvenile-to-adult ratio. Large cypress domes have higher juvenile-to-adult ratio than small cypress domes. There is higher recruitment at the edge of the wetland than in the centre. Ranchland cypress domes have a higher juvenile-to-adult ratio than managed-forest cypress domes.

recruit in 100 years, which constitutes a fraction of a life span for a cypress tree. We project that *c.* 89% of the currently recruiting cypress populations in cypress domes will fail to recruit in 100 years (in the year 2104) and that most (87%) remaining cypress populations that still recruit will be on ranchland (Table 3).

Discussion

Surprisingly, we found that managed-forest and urban cypress domes had similar low cypress recruitment. We believe that different factors may be causing this outcome in each land-use category and that this is important for the management of cypress in those areas. In addition, we found that ranchland cypress domes generally maintained higher recruitment; they may thus be important sources of cypress reproduction in the future. The main factors relating to cypress recruitment were time since urbanization (among urban land-use classes), distance to the wetland edge, wetland area and urbanization level. In urban areas, recruitment persisted until about 20 years after urbanization of lands surrounding a cypress population, after which it ceased, causing biological inertia in urban cypress domes.

Alterations to both hydrology and fire regimes are common in urban areas (Sharitz *et al.* 1992; Russell, Van Lear & Guynn 1999; Ehrenfeld 2000; Faulkner 2004; Kentula, Gwin & Pierson 2004) and important to cypress populations (Penfound 1952; Brandt & Ewel 1989; Burns & Honkala 1990; Casey & Ewel 2006). As direct measurements of these processes were impossible, the amount of urbanization and time since urbanization were used to measure changes to hydrological and fire regimes as well as other changes typical of urbanization, including increases in pollutants, nutrients and sedimentation. All of these alterations occur within the life span of a cypress tree in a rapidly urbanizing area such as greater Orlando and are likely the ultimate mechanisms reducing cypress recruitment in urbanized areas.
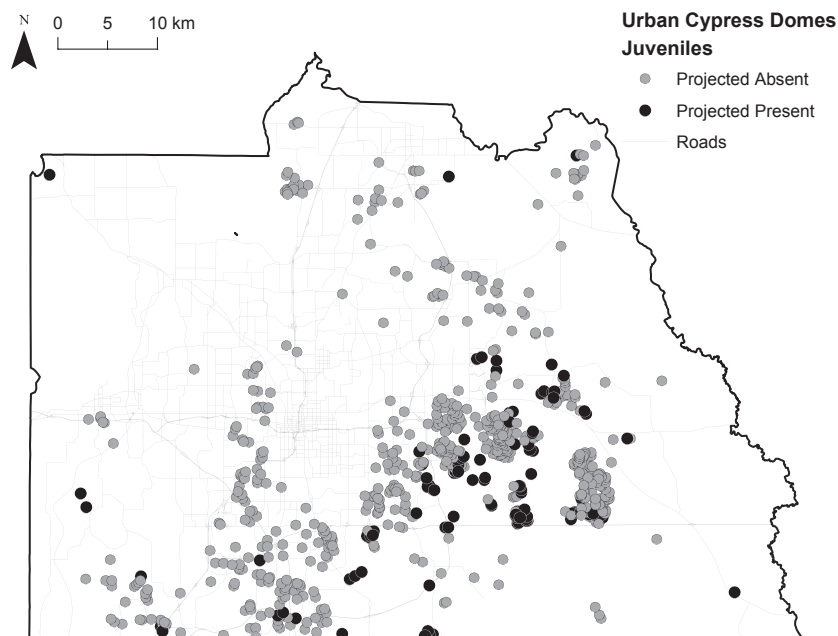
Fig. 5. Projected juvenile presence and absence for urban cypress domes in 2004. High road density represents the more urbanized portions of the study area. Cypress domes that have projected juvenile presence are on the periphery of the urban area.

Table 3. Projections of recruiting cypress domes in central Florida through 2104

	In 2004		In 2104	
	Total remaining	Total recruiting	Total remaining	Total recruiting
Managed forest	891	576	28	18
Ranchland	1189	769	219	142
Urban	730	115	206	4
Total	2810	1460	453	164

Conversion calculations: 25·8% of managed forest converted to urban every 20 years, 3·1% of ranchland converted to urban every 20 years (after 20 years urban domes cease recruiting); loss calculations: 24·2% of managed forest lost every 20 years, 25·6% of ranchland lost every 20 years, 39·2% of urban lost every 20 years; recruitment calculations: 64·7% of managed-forest/ranchland recruiting (based on juvenile-to-adult ratio <0·5) and 15·7% of urban domes newer than 20 years recruiting (based on presence/absence predictions), no urban domes older than 20 years recruiting.

However, managed-forest cypress domes also showed lower recruitment rates, and we speculate that an altered fire regime could be leading to reduced recruitment in these areas. In natural fire regimes, fire in the surrounding upland may also burn wetlands, at least partially, and especially in wetlands with seasonal hydroperiods (Frost, Walker & Peet 1986). We observed several cypress domes in managed forests with fire breaks at their edges that would prevent upland fires from burning into the wetland. Managers of forests have used fire breaks to avoid muck or peat fires that can generate persistent smoke and pose a reignition risk for several weeks (Reardon, Hungerford & Ryan 2007; Leeds, Garrett & Newman 2009) – a severe problem to be avoided near a metropolitan region. Our observations indicate that fire management practices in forests could be preventing fire in cypress domes, and this could lead to lower cypress recruitment in those areas. The recruitment levels in managed-forest cypress domes are equivalent to those seen in urbanized cypress domes where lower recruitment may result from multiple factors including *both* hydrological and fire regime change. We

infer that fire regime is an under-appreciated force maintaining cypress populations. Cypress domes with relatively short hydroperiods (i.e. substantial periods of oxidative soil conditions) are unlikely to accrue substantial organic matter and should not cause muck or peat fires. Those wetlands do not need fire breaks and should be subjected to prescribed fires to help restore and maintain cypress recruitment, much like other vegetation.

Fire breaks were not present in the ranchland cypress domes we sampled. Prescribed fires, in addition to grazing, soil disturbance, exotic weed control, chemical applications and mechanical removal are common in cattle ranches and result in suppressed woody vegetation and forage grass growth in pastures (Morrison & Humphrey 2001; Main *et al.* 2004; Ansley *et al.* 2010). These practices may mimic natural fire regimes and maintain recruitment in ranchland cypress domes better than prescribed fire practices in managed forests. In other systems, livestock grazing has also been found to maintain some natural landscape structure, and cattle ranches have been found to be valuable reserves of biodiversity, especially in highly urbanized regions

(Curtin 1995; Morrison & Humphrey 2001; Main *et al.* 2004). Our results support the value of ranchlands for regional biodiversity, specifically in this case for the cypress wetlands embedded in cattle ranches.

Urban cypress domes experience virtually no fire and often have strongly altered hydrology (either becoming permanently flooded or drained) relative to the variable hydrology of non-urban wetlands (Sharitz *et al.* 1992; Russell, Van Lear & Guynn 1999; Ehrenfeld 2000; Faulkner 2004; Kentula, Gwin & Pierson 2004). Alterations common in urban areas appear to be consistent across the three levels of urbanization (low-intensity, medium-intensity or high-intensity) because urbanization levels were far less important to cypress recruitment than was time since urbanization. Recruitment dropped substantially around 20 years post-urbanization; none of the sampled cypress domes >20 years post-urbanization (range: 22–60 years) showed recruitment. With large cypress seed crops every 3–5 years (U.S. Department of Agriculture Forest Service 1974), we would expect multiple cohorts of juveniles to have recruited in cypress domes 22–60 years post-urbanization. While the time required for a tree to reach 2 m (and be classified as an adult in this study) is unknown and likely depends on nutrient availability, we estimate it may be <10 years. Thus, if recruitment was occurring in cypress domes 20 years post-urbanization, juveniles should have been present.

Prior to *c.* 20 years after urbanization, the most important variable in determining the presence or absence of juveniles is distance to the edge of the wetland. This result is consistent with the fact that many urban cypress domes are used for stormwater retention and hold more water longer in the centre, permitting germination only on the edge of the wetland. This pattern continues for about 20 years post-urbanization, after which there is likely encroachment of other vegetation (including upland vegetation and invasive species) in the absence of fire that halts cypress recruitment altogether. Cypress recruitment virtually ceases but the adult trees remain and the remaining populations exhibit biological inertia.

Wetland area and distance to the wetland edge were the most important variables to predict juvenile-to-adult ratio in managed-forest and ranchland cypress domes. Larger cypress domes have more edge and often longer hydroperiods allowing for standing water in the centre and increased saturation of the soil near wetland edges. Saturated but not flooded soils are ideal for cypress germination and seedling survival (Brandt & Ewel 1989; Burns & Honkala 1990). The effect of wetland size on cypress recruitment in managed-forest and ranchland cypress domes was likely due to more area with more suitable hydrology and reduced competition at the edge as a result of frequent prescribed fire (provided there were no fire breaks).

Overall, current management in forested lands and essentially permanent changes in urbanized areas will lead to biological inertia in hundreds of cypress populations within the Orlando metropolitan area (McCauley, Jenkins & Quintana-Ascencio 2012) causing an extinction debt for the species in this area. Given that Orlando urbanization rates mirror those in other metropolitan areas in the region (McCauley, Jenkins & Quintana-Ascencio 2012), the extinction debt may be regional. It is unrealistic to expect urban areas to introduce flooding and fire to restore conditions for recruitment in cypress populations. Reduced urban sprawl is the only practical means to mitigate the ongoing recruitment failure in cypress populations in the area, and likely elsewhere in the cypress range.

Management practices in forests are far more amenable to change, and a change in prescribed fire practice (i.e. burning through cypress domes with seasonal or ephemeral hydroperiods) could permit ongoing cypress recruitment and reverse the extinction debt of this species. This simple change in practice could strongly affect recruitment and long-term viability of this dominant, long-lived species and other wetland species dependent on these ecosystems, in many wetlands of the south-eastern United States. In addition, cattle ranches may substantially contribute to the continued recruitment of cypress and other species in remaining wetlands. In the absence of a change in forest management practice and preservation of ranchland, thousands of wetlands may remain in the south-eastern United States in the foreseeable future, but cypress will fail to recruit within decades in many wetlands. In that case, the once typical and valued cypress domes could be replaced by upland vegetation, with unknown consequences for regional ecosystem services and biodiversity.

Acknowledgements

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