2016

Determinants of spread in an urban landscape by an introduced lizard

Jason J. Kolbe
University of Rhode Island, jjkolbe@uri.edu

Paul VanMiddlesworth

See next page for additional authors

Citation/Publisher Attribution

Kolbe, J.J., VanMiddlesworth, P., Battles, A.C. et al. Landscape Ecol (2016) 31: 1795. https://doi.org/10.1007/s10980-016-0362-1
Available at: https://doi.org/10.1007/s10980-016-0362-1

Authors
Jason J. Kolbe, Paul VanMiddlesworth, Andrew C. Battles, James T. Stroud, Bill Buffum, Richard T. T. Forman, and Jonathan B. Losos

Determinants of spread in an urban landscape by an introduced lizard

Jason J. Kolbe • Paul VanMiddlesworth • Andrew C. Battles • James T. Stroud •
Bill Buffum • Richard T.T. Forman • Jonathan B. Losos

J. J. Kolbe (Corresponding author) • A. C. Battles
Department of Biological Sciences, University of Rhode Island, 120 Flagg Rd.,
Kingston, RI, 02881, USA
e-mail: jjkolbe@uri.edu
phone: 401-874-9731

P. VanMiddlesworth • J. B. Losos
Department of Organismic and Evolutionary Biology and Museum of Comparative
Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138, USA

J. T. Stroud
Department of Biological Sciences, Florida International University, Miami, FL,
33199, USA

B. Buffum
Department of Natural Resources Science, 1 Greenhouse Rd., University of Rhode
Island, Kingston, RI, 02881, USA

R. T. T. Forman
Graduate School of Design, Harvard University, 48 Quincy St., Cambridge, MA,
02138, USA

Date of the manuscript draft: November 2, 2015

Revised version of the manuscript submitted:

Revised manuscript word count: 7,262

Abstract

Context

Urban landscapes are a mixture of built structures, human-altered vegetation, and remnant semi-natural areas. The spatial arrangement of abiotic and biotic conditions resulting from urbanization doubtless influences the establishment and spread of non-native species in a city.

Objectives

We investigated the effects of habitat structure, thermal microclimates, and species coexistence on the spread of a non-native lizard (*Anolis cristatellus*) in the Miami metropolitan area of South Florida (USA).

Methods

We used transect surveys to estimate lizard occurrence and abundance on trees and to measure vegetation characteristics, and we assessed forest cover and impervious surface using GIS. We sampled lizard body temperatures, habitat use, and relative abundance at multiple sites.

Results

At least one of five *Anolis* species occupied 79% of the 1,035 trees surveyed in primarily residential areas, and non-native *A. cristatellus* occupied 25% of trees. Presence and abundance of *A. cristatellus* were strongly associated with forest patches, dense vegetation, and high canopy cover, which produced cooler microclimates suitable for this species. Presence of *A. cristatellus* was negatively associated with the ecologically similar non-native *A. sagrei*, resulting in reduced abundance and a shift in perch use of *A. cristatellus*.

Conclusions

The limited spread of *A. cristatellus* in Miami over 35 years is due to the patchy, low-density distribution of wooded habitat, which limits dispersal by diffusion. The presence of congeners may also limit spread. Open habitats — some parks, yards and roadsides — contain few if any *A. cristatellus*, and colonization of isolated forest habitat appears to depend on human-mediated dispersal.

Keywords

Anolis - body temperature - canopy cover - GIS - forest cover - impervious surface - thermal microclimates - tree characteristics - urban heat island - urban vegetation

Introduction

Upon arrival in a city, non-native species encounter a spatially heterogeneous environment that varies in the types and densities of buildings, vegetation, infrastructure, and remnant natural areas (Pickett et al. 2001; Cadenasso et al. 2007; Forman 2014). This variability in habitat structure and its spatial patterning will likely influence the ability of invaders to establish and spread within an urban area. For example, exotic grey squirrels in the UK are positively associated with increased canopy cover, larger trees, and the presence of seed-bearing trees as well as supplementary feeders for birds (Bonnington et al. 2014). Thus, the arrangement of vegetation and non-vegetative features within the urban landscape influences where exotics establish and the routes by which they spread. Identifying those features associated with the occurrence of exotic species is important for understanding their current distributions and potential for future spread.

As a consequence of habitat structure modification during urbanization, city temperatures can be several degrees higher than surrounding rural areas (Akbari et al. 2001; Arnfield 2003; Chen and Jim 2008; Rizwan et al. 2008). These urban heat islands are spatially and temporally heterogeneous (Ramalho and Hobbs 2011), reflecting variation in the matrix of built structures and local vegetation and creating a thermal mosaic (Georgi and Zafiriadis 2006; Hamdi and Schayes 2008; Huang et al. 2008). This variation influences the microclimates available in a city, including air and surface temperatures, relative humidity, solar radiation, and wind speed. Thermal microclimates are critically important to ectotherms (e.g., insects, lizards, frogs), which rely on external sources of heat to regulate their body temperatures. Because temperature is fundamentally important for development, growth, survival, and reproduction in ectotherms (Angilletta 2009), organisms living in a city are likely to be sensitive to variation in vegetation and urban features that affect thermal microclimates (Ackley et al. 2015a).

In addition to the habitat structure of a city, interactions with potential competitors and predators can influence occurrence and abundance patterns (Shochat et al. 2006; Anderson and Burgin 2008). For example, abundance of a native gecko, *Lepidodactylus lugubris,* throughout the Pacific is strongly influenced by interactions with a competitively superior non-native gecko, *Hemidactylus frenatus* (Case et al. 1994), which better exploits insect resources concentrated under artificial night lighting (Petren and Case 1996). In general, more ecologically similar species are predicted to have stronger negative effects on each other at local scales through competition (Pianka 1981; Losos 1994). Thus, both biotic and abiotic factors may influence the establishment, spread, and ultimately the distribution of non-native species in a city.

In this study, we investigate the effects of habitat structure, thermal microclimates, and species interactions on the spread of introduced *Anolis* lizards in the Miami metropolitan area. Our study group, *Anolis* lizards (or anoles), comprise a species-rich genus of small, insectivorous, diurnal lizards found in the Neotropics from the southeastern United States to South America including Caribbean islands (Losos 2009). Many *Anolis* species occupy both natural and human-modified areas in their native and non-native ranges (Perry et al. 2008; Irschick et al. 2005; Marnocha et al. 2011; Kolbe et al. 2015). There are nine *Anolis* species established in Miami, only one of which — *A. carolinensis* — is native to the U.S. (Lever 2003; Kolbe et al. 2007; Kraus 2009). Four species have very restricted distributions (*A. chlorocyanus*, *A. cybotes*, *A. garmani* and *A. porcatus*), two are distributed throughout the Miami area (*A. distichus* and *A. equestris*), and one is found throughout Florida, the Gulf Coast, and southern Georgia and South Carolina (*A. sagrei*). In contrast to these either very restricted or widespread species, an eighth non-native species, *A. cristatellus* (Fig. 1, inset), is expanding its distribution in Miami, but is not yet ubiquitous. We can therefore identify factors related to its current distribution and predict whether future spread in urban areas is likely.

Anolis lizards have a number of advantages for this study. First, anoles in Miami are conspicuous, easy to detect, and sufficiently different in ecology and morphology to accurately identify to species when present. Second, the introduction history of *A. cristatellus* in Miami is well studied with two independent introductions from its native range in Puerto Rico (Kolbe et al. 2007). Third, the other four *Anolis* species that co-occur with *A. cristatellus* in Miami — *A. carolinensis*, *A. distichus*, *A. equestris* and *A. sagrei* — were all present prior to its introduction in the mid-1970s. These species span a range of ecological similarity; specifically, *A. sagrei* and *A. distichus* typically perch lower to the ground on tree trunks, similar to *A. cristatellus*, whereas *A. carolinensis* and *A. equestris* perch higher in the canopy (Losos 2009). We can therefore test the hypothesis that more ecologically similar congeners influence the presence of *A. cristatellus* in Miami. Lastly, the thermal biology of anoles in general, and *A. cristatellus* in particular, is well studied (Losos 2009). Previous studies detail the thermal preferences, thermal tolerances, and field body temperatures of *A. cristatellus* from numerous sites in Puerto Rico and Miami (e.g., Huey 1974; Huey and Webster 1976; Hertz 1992; Leal and Gunderson 2012; Kolbe et al. 2012; Gunderson and Leal 2012), allowing us to evaluate if the effects of urban vegetation on thermal microclimates are relevant to *A. cristatellus*.

A primary goal of this study is to contrast how abiotic and biotic aspects of the urban environment influence the current distribution and abundance of a recently introduced species to better understand its potential for future spread. We survey lizards and vegetation characteristics on a tree-by-tree basis using transects across putative distribution boundaries, and test for relationships at the landscape level between the presence of *A. cristatellus* and GIS-based data attributes of forest cover and impervious surfaces. We predict that 1) urban vegetation structure and arrangement will influence the occurrence and abundance of *A. cristatellus*. In particular, we predict that *A. cristatellus* will be associated with denser vegetation and forested areas, which produce relatively cooler microclimates. Based on previous ecological studies (Losos 2009), we also predict 2) negative associations between *A. cristatellus* and its more ecologically similar congeners in Miami. Specifically, *A. sagrei* and *A. distichus* overlap most with *A. cristatellus* in their structural microhabitat (i.e., the height, diameter, and type of perch), which should lead to stronger interspecific competition.

Methods

Study area

We conducted this study in the Miami metropolitan area, where the initial sites of introductions for *A. cristatellus* are documented. Genetic analyses confirmed two independent introductions from geographically and genetically distinct native-range sources in Puerto Rico (Kolbe et al. 2007). The Key Biscayne population is from San Juan, Puerto Rico and was first detected in a residential area on the island in 1975 (Schwartz and Thomas 1975; Bartlett and Bartlett 1999). The South Miami population is from northeast Puerto Rico and was found in a different residential area in 1976 (Wilson and Porras 1983). The Key Biscayne population is ~5 km from the mainland population separated by a bridge to Virginia Key and the Rickenbacker Causeway to the mainland. The two introduction sites are ~12 km apart across Biscayne Bay. The bulk of the study area is residential with detached single units, considerable tree cover, and low-traffic, two-lane roads. Also present are commercial districts, high-traffic roads up to six lanes, open parklands, urban forests, and waterways such as canals, lakes, and coastal areas (Fig. 1, Supplementary Fig. 1).

Study design and sampling

In summer 2009, we collected preliminary data on *A. cristatellus* presence in the Miami area by conducting block-by-block walking surveys radiating from the initial points of introduction in South Miami and Key Biscayne. Based on these data, we established five 610 m x 1100 m plots in South Miami, each crossing an observed transition from presence to absence of *A. cristatellus*. In each plot, we established three to six roadside transects running perpendicular to the transition zone

(Supplementary Fig. 2). On our initial visit to each transect in June 2010, we measured tree characteristics (Table 1) and, using binoculars when needed, observed *Anolis* lizards on trees with a trunk diameter >10 cm growing in the roadside public right-of-way. Although lizards use smaller trees, the availability of such trees was limited along roadsides and in yards. All species have multiple diagnostic features, which aided accurate species identification. Following this initial survey, we returned to each transect two more times to survey the same trees for the presence and total number of lizards of the five *Anolis* species. One to three trained observers were present for each survey, with at least two observers in most cases. Data from these transects were used to evaluate whether the presence of *A. cristatellus* was related to the presence of congeners and to the characteristics of the trees and surrounding vegetation (Table 1).

Given patterns of species coexistence from these transects, we conducted visual encounter surveys to determine if congener presence affects the relative abundance and habitat use of *A. cristatellus* (Crump and Scott 1994; Kolbe et al. 2008). Surveys consisted of walking at a constant pace for 15 minutes and recording the species, time, sex, and perch characteristics (i.e., height and diameter) for all undisturbed lizards observed. We compared relative abundance at sites with predominantly *A. cristatellus* (n=10 surveys) to sites with *A. distichus* and *A. sagrei* in addition to *A. cristatellus* (n=6 surveys). Because *A. distichus* and *A. sagrei* co-occur throughout most of Miami, we were unable to find nearby sites with only one of these species. We supplemented data on perch characteristics with opportunistic observations of all three species at the same sites.

The presence-absence data from transects, visual encounter surveys, and opportunistic surveys allowed us to map the distribution of *A. cristatellus* in Miami (Figs. 1 and 2). In addition to the intensive sampling within the core areas of South Miami and Key Biscayne, we also investigated potential localities throughout Miami-Dade County including municipal parks and regional waste transfer stations. Preliminary surveys showed *A. cristatellus* was present in forest patches in some parks associated with waste transfer stations, suggesting transport of yard waste from houses to regional stations as a potential dispersal mechanism.

GIS analysis of forest cover and impervious surfaces

To complement analyses based on transect data, we conducted a geographic information system (GIS) analysis of the study area using ArcGIS version 10.2 (Environmental Systems Research Institute, Redlands, CA) and publicly available GIS layers of impervious surface (MRLC 2011) and forest fragmentation (NOAA 2010). The MRLC Percent Developed Imperviousness layer, a raster dataset with 30-meter pixels, provides the average percentage of human-made impervious surface for each pixel. The NOAA forest fragmentation layer, a raster dataset with 30-meter pixels, distinguishes between four fragmentation types: 1) "core forest" refers to forested pixels that are not adjacent to any non-forested pixels, 2) "patch forest" refers to forested pixels in small patches that are not large enough to contain a 90m x 90m block of forest, 3) "perforated forest" refers to forested pixels adjacent to small non-forested patches that are not large enough to contain a 90m x 90m block of non-forested area, and 4) "edge forest" refers to forested pixels adjacent to larger non-forested patches that contain at least one 90m x 90m block of non-forested area. We used GIS to generate 11 attributes describing forests and impervious surfaces (Table 2).

Thermal microclimates and lizard body temperatures

To investigate the range of possible thermal microclimates available to *A. cristatellus* in Miami during peak summer temperatures, we measured the temperature under two trees—one with an open canopy (*Thrinax radiata*, DBH = 12 cm) and another with a heavily shaded canopy (*Chukrasia tabularis*, DBH = 145 cm). We used painted, hollow, copper models the size of lizards with an iButton inside to estimate temperatures a lizard would experience in each location without behavioral or physiological thermoregulation (Hertz 1992; Gunderson and Leal 2012; Ackley et al. 2015a). Temperatures were recorded every 15 minutes on the north, south, east, and west sides of each tree at a height of 1.5 m from 1700 h on July 17 to 1000 h on July 21, 2014. To estimate the percentage of open canopy, we took hemispherical canopy photographs in each cardinal direction using a 180° fisheye lens and analyzed them using Gap Light Analyzer version 2.0 (Frazer et al. 1999).

To estimate the range of field body temperatures (T_b) for *A. cristatellus* in Miami, we sampled lizards and random locations at three sites that varied in species composition and vegetative structure. For comparative purposes, we also sampled *A. sagrei*, which has both higher field T_b and thermal tolerances than *A. cristatellus* (Corn 1971; Lee 1980; Gunderson and Leal 2012; Kolbe et al. 2012, 2014). The sites included a bike path along a canal where both species were sampled, a residential area where only *A. sagrei* was sampled, and a forested area where only *A. cristatellus* was sampled. For each undisturbed lizard captured, we recorded T_b, air temperature 1 cm above the substrate where the lizard was perched, and copper lizard model temperature at the same location as the lizard using a thermocouple probe connected to a digital thermometer (Omega HH802U). We then took a hemispherical canopy photo to estimate canopy openness as described above. For comparison, we took copper lizard model temperature, air temperature, and a canopy photo at randomly selected locations within each study site. Lizard T_b and random location data were collected between 0800 to 1400 h, which is a high-activity time of day during the summer.

Data analysis

Occupancy and estimates of detection probabilities were calculated using single season occupancy models (MacKenzie et al. 2002) in the program PRESENCE (Hines 2006). Likelihood models calculated in PRESENCE all assume that 1) any site where a species is present remains occupied, 2) species may or may not be detected when present, but are not detected when absent, and 3) the detection of a species at one sampling site is independent of detection at all other sites (MacKenzie et al. 2002). A minimum of two sample occasions is required for model estimation. We conducted three repeat surveys at each sampling point. Occupancy models to calculate estimates of detection were produced with all surveyors (Rick Stanley [RS], PV, and JJK) independently as covariates as well as using full identity models including all surveyors.

We used generalized linear models (GLM; McCullagh and Nelder 1989; R 2013) with binomial (presence-absence) and continuous (abundance) response variables. This allowed us to form linear and quadratic relationships between the response and explanatory variables (Broennimann *et. al.* 2012), which were standardized to normalize their distributions. Explanatory variables included the tree characteristics of trunk diameter, canopy diameter, distance to nearest plant, distance to nearest tree, and overstory canopy cover (Table 1). Model selection was performed using a stepwise procedure based on the Akaike information criterion (AIC; Akaike 1974). We conducted three separate analyses using presence-absence as the response variable. First, we compared transect sections with *A. cristatellus* present (but not necessarily occupying every tree) versus sections where *A. cristatellus* was absent; second, we compared the presence versus absence of *A. cristatellus* on all trees pooled; and third, we compared the presence versus absence of *A. cristatellus* on trees within only the sections of transects with *A. cristatellus* present. We then repeated the latter two analyses using *A. cristatellus* abundance as the response variable.

When analyzing the GIS-based attributes, we conducted two separate analyses. First, we divided street blocks from each transect into those with *A. cristatellus* present versus absent and compared attributes derived from GIS (Table 2). Second, we used presence and absence points for individual observations throughout the Miami metropolitan area to test for relationships with GIS-derived attributes, restricting the data set to no more than one observation per block.

For categorical explanatory variables (Table 1), we used likelihood ratio tests to compare tree characteristics between sections of transects with *A. cristatellus* present versus absent. When evaluating *A. cristatellus* abundance in relation to categorical tree characteristics, we used t-tests or analyses of variance (ANOVA) as appropriate. We tested for a relationship between the presence-absence of *A. cristatellus* and the presence-absence of the four congeners using likelihood ratio tests. We tested for effects using all trees sampled, as well as only those trees on the sections of transects with *A. cristatellus* present. Analyses were conducted for trees on each plot separately and with trees from all plots pooled.

Relative abundances from the visual encounter surveys were not normally distributed, so we used a Wilcoxon test to evaluate whether differences existed between sites. In particular, we predicted relative abundance of *A. cristatellus* would decrease when it is with other *Anolis* species compared to being alone. Log-transformation achieved normality for perch height and diameter, and we tested for a difference in these perch characteristics for *A. cristatellus* between sites with and without congeners using t-tests.

We compared lizard T_b and copper lizard model temperatures at the same locations using linear regression. Using this calibration, we adjusted model temperatures to make them directly comparable to lizard T_b for both species. We averaged model temperatures by hour and plotted them against time of day. We compared these model temperature estimates (i.e., non-thermoregulating lizards) to field T_b collected at the same time of year, and literature estimates of preferred T_b and high temperature tolerance (i.e., critical thermal maximum, or CTmax) for *A.*

cristatellus (Huey and Webster 1976). To investigate variation in field T_b of lizards, we conducted an analysis of covariance (ANCOVA) testing for differences among groups (i.e., *A. cristatellus*, *A. sagrei*, and random locations) with air temperature, time of day, and canopy openness as covariates. We used the Johnson-Neyman procedure (White 2003) to determine the range of covariate values in which temperatures differed between groups when regression slopes were heterogeneous (i.e., a significant interaction between the main effect and covariate).

Results

Anolis cristatellus distribution in Miami

The combination of opportunistic surveys, visual encounter surveys, and transects resulted in fine-scale distribution data for *A. cristatellus* in key parts of the Miami metropolitan area (n=362 presence points and n=483 absence points; Fig. 1, Supplementary Fig. 1). This species has expanded its core range from the original point of introduction no more than 2 km to the west, south, and east in South Miami, and ~7 km to the northeast. A six-lane highway (i.e., the Dixie Highway/US 1) to the northwest of the core South Miami distribution appears to limit unaided dispersal. The introduction to Key Biscayne expanded across the majority of the island, but not across the bridge to Virginia Key or causeway to mainland Miami.

We detected seven disjunct populations ranging from < 1 to 20 km from the core distribution in South Miami. These sites included several Miami-Dade County Parks (i.e., Chapman Fields, Kendall Indian Hammock, and Oak Grove) as well as the University of Miami campus and three residential areas. We found *A. cristatellus* at two of 13 waste transfer stations in Miami-Dade County (i.e., Chapman Fields and Sunset Kendall), but only when adjacent to forested parks. Most waste transfer stations had only a few widely spaced trees and were surrounded by residential or commercial areas. Other species were present at all waste transfer stations with *A. distichus* and *A. sagrei* being the most common.

Tree characteristics

Transect surveys yielded observations on a total of 1035 trees. At least one anole was present on 79% of the trees, and *A. cristatellus* occupied 25% of the trees (Table 3). The best models to estimate detection probabilities for each species were single season occupancy models including all three surveyors. Estimates of among-surveyor detection probability for the focal species, *A. cristatellus*, ranged from 0.50-0.96 among sites, and average detection probability for each surveyor for all sites was estimated at 0.63-0.90 (Supplementary Table 1). Total detection probability for the full model (all surveyors) was estimated at 0.88 (±0.12). These estimates for detection were high and therefore detection probabilities were not considered influential in subsequent analyses. The most likely models of tree characteristics found *A. cristatellus* associated with trees having larger trunks, larger canopies, greater percent of overstory canopy cover, and closer to other plants and trees (Tables 1 and 4). These results suggest that *A. cristatellus* occupies relatively shady and densely vegetated areas.

Sections of transects with *A. cristatellus* present had a greater proportion of native trees (X^2=12.3, df=1, P<0.001, n=937) and trees with smooth bark (X^2=14.4, df=4, P<0.01, n=1035) as compared to transect sections with *A. cristatellus* absent.

In contrast, transect sections with and without *A. cristatellus* did not differ in the proportion of palm trees (X^2=0.5, df=1, P=0.46, n=1028) or the number of trunks on trees (X^2=4.3, df=2, P=0.12, n=1035).

Models for the abundance of *A. cristatellus* showed similar results with increased abundance associated with trees having larger trunks and canopies, greater percent of canopy cover, and closer to other plants (Table 4). *Anolis cristatellus* abundance was twice as high on non-palm compared to palm trees (t=2.7, df=1026, P<0.01) and highest on trees with multiple trunks ($F_{2,1032}$=14.9, P<0.0001), which were often large *Ficus* trees. Abundance did not differ between native and non-native trees (t=-1.08, df=935, P=0.28) or among bark textures ($F_{4,1030}$=1.57, P=0.18).

Analyses of *A. cristatellus* presence using GIS-based attributes were consistent with transect surveys. Blocks with *A. cristatellus* present had more trees per km, greater canopy cover, denser vegetation, and less impervious surface area (Table 5A). Similarly, when analyzing the presence-absence points across Miami, *A. cristatellus* was present at locations with less impervious surface and closer to larger blocks of forest but not smaller forest patches (Fig. 2; Supplementary Fig. 3; Table 5A). The percentage of forested area was three times greater in the core area of *A. cristatellus'* distribution compared to the study area as a whole (Supplementary Table 2). Moreover, the percentage of the core area with high impervious surface (> 40%) was about half as much as the study area as a whole (Supplementary Table 2).

Congener presence

Pooling all trees sampled, *A. distichus* and *A. sagrei* were both significantly more likely to be absent when *A. cristatellus* was present than expected by chance, with effects involving *A. sagrei* being much stronger (Table 6A). The presence of *A. carolinensis* or *A. equestris* had no effect. When evaluating each plot separately, a negative effect was observed with *A. sagrei* for most plots, and with *A. carolinensis* and *A. distichus* in a few plots (Table 6A). This suggests congeneric interactions may differ among plots. All comparisons for individual transects were non-significant (results not shown).

Dividing each transect into sections based on *A. cristatellus* presence or absence, only *A. sagrei* was more likely to be absent where *A. cristatellus* was present (Table 6B). There was no interaction with the less abundant species *A. carolinensis* and *A. equestris*. In contrast to the analyses of all trees pooled, this analysis revealed no relationship between occurrence of *A. distichus* and *A. cristatellus* (Table 6B). Potential interactions for *A. cristatellus* appear to be strongest with *A. sagrei*, followed by *A. distichus*, but little evidence existed for interactions with *A. carolinensis* or *A. equestris.*

Relative abundance and habitat use

Relative abundance estimates from visual encounter surveys were consistent with the negative relationship between the presence of *A. cristatellus* and two of its congeners in Miami. *Anolis cristatellus* was four times more abundant at sites with no congeners than in sites occupied by *A. distichus* and *A. sagrei* (mean±SE: 45.3±2.5 versus 11.0±3.2 per survey; Wilcoxon: Z = 3.21, P<0.01). Furthermore, at sites with congeners, *A. cristatellus* perched nearly twice as high (mean±SE: 79.0±4.2 v. 47.2±1.8; t=6.38, df=608, $P<0.0001$) and on trunk substrates twice as wide (mean±SE: 18.6±1.5 v. 9.5±0.67; t=6.1 df=604, $P<0.0001$), suggesting a possible shift in habitat use in the presence of congeners.

Thermal microclimates and lizard body temperatures

We investigated the thermal consequences of canopy cover by comparing copper lizard model temperatures under trees with open versus shaded canopies. The percentage of overstory canopy cover ranged from 31-46% for the open canopy tree versus 89-91% for the shaded canopy tree (Supplementary Fig. 4). Model temperatures for the two trees were similar through the night from ~1900 h to ~0800 h (Fig. 3). After 0800 h, model temperatures on the open canopy tree increased quickly, exceeding both shaded tree temperatures and preferred temperatures of *A. cristatellus* from 1000-1800 h. While there was little variation in model temperatures among the sides of the shaded tree, temperatures on the sides of the open tree differed substantially from one another, with a maximum difference of 5.7°C at 1000 h.

Lizard T_b and model temperatures showed a strong positive correlation ($r=0.91$; $P<0.0001$, $n=52$), suggesting that models accurately reflected lizard body temperatures. ANCOVA results showed all three covariates had significant positive effects on T_b/model temperatures (canopy openness: $F_{1,83}=46.42$, $P<0.0001$; air temperature: $F_{1,83}=7.97$, $P=0.006$; time of day: $F_{1,83}=23.51$, $P<0.0001$; whole model $R^2=0.67$). *Anolis sagrei* field body temperatures (mean±SE: 31.2°C±0.4) were significantly higher than *A. cristatellus* temperatures (mean±SE: 28.8°C±0.4; $F_{2,83}$=3.79, P=0.03; Tukey's HSD post hoc test P<0.05; Fig. 4). However, because the species by canopy openness interaction was significant this main effect should not be interpreted directly but only in conjunction with the covariate. The relationship between temperature and canopy openness had a much steeper slope for *A. cristatellus* compared to *A. sagrei* and random points (P<0.05 for comparison of slopes; Fig. 4). The Johnson-Neyman procedure supported T_b differences between *A. cristatellus* and both *A. sagrei* and random points for relatively closed canopies (i.e., < 15% openness). In summary, all covariates had significant effects on lizard T_b, but *A. cristatellus* had lower T_b compared to *A. sagrei* and the two species appeared to thermoregulate differently in closed canopy areas.

Discussion

Since its introduction to South Miami over 40 years ago, *A. cristatellus* has spread only modestly by diffusion (~0.2-0.25 km/yr), much slower than some of the other introduced *Anolis* species in Miami and invasive species in general (Lockwood et al. 2007; Davis 2009). A recent analysis shows an order of magnitude faster spread rates on average for exotic lizards and snakes (~3 km/yr) and invaders to the Nearctic (~5 km/yr; Liu et al. 2014). Results from our study suggest that both abiotic and biotic factors contribute to the limited spread of *A. cristatellus* in urban Miami. The fragmentation of suitable habitat is an abiotic constraint. The presence of *A. cristatellus* is strongly associated with forest habitats, which result in cooler and more humid microclimates (e.g., Wong and Yu 2005; Georgi and Zafiriadis 2006;

Millward et al. 2014; Ackley et al. 2015a; Fig. 3). Because forests are patchily distributed in Miami (Fig. 2a), dispersal by diffusion will be limited by fragmentation caused by canals, non-forest habitats, and areas of impervious surface, such as buildings, roads, and parking lots (Fig. 2). Therefore, human-mediated dispersal may be an important mechanism for moving *A. cristatellus* to isolated patches of suitable habitat, which lizards are unable to reach via natural diffusion.

Interactions with ecologically similar congeners may be a biotic constraint. *Anolis cristatellus* is spreading into areas occupied by one or more additional *Anolis* species. As expected, we found negative associations between *A. cristatellus* and ecologically similar *A. sagrei* and *A. distichus*, but weak or no relationship between the occurrence of *A. cristatellus* and *A. carolinensis* or *A. equestris*, which typically perch higher in the canopy (Losos 2009). Ultimately, the relative abundance of each species and the extent to which they overlap on niche axes, such as structural habitat and thermal microclimate, will determine whether and how quickly *A. cristatellus* spreads to new areas.

Effect of urban vegetation on the spread of A. cristatellus

The presence and abundance of introduced *A. cristatellus* in Miami are positively associated with larger trees, denser vegetation, greater canopy cover, proximity to forest, and less impervious surface. These features are indicative of forest patches in the urban environment including parks and certain residential areas. Previous studies show patterns of urban vegetation can be related to numerous factors including socio-economics, remnant natural habitats, and neighborhood age and history (e.g., Nowak et al. 1996; Martin et al. 2004; Grove et al. 2006; Jenerette et al. 2007; Luck et al. 2009; Boone et al. 2010; Forman 2014). *Anolis cristatellus* was present in several tropical hardwood hammocks, including parks outside of its core distribution in South Miami. These disjunct populations suggest dispersal limitation, not lack of suitable habitat, slows the spread of *A. cristatellus* outside its core area in South Miami. The patchwork of scarce suitable forested habitat in Miami will continue to limit the spread of *A. cristatellus* by diffusion, making human transport an important dispersal mechanism. The presence of *A. cristatellus* at forested parks located adjacent to spatially isolated regional waste transfer stations suggests yard waste collection and transport may be one such method of dispersal.

Vegetation in some residential areas within the core distribution of *A. cristatellus* can change rapidly over short distances, likely affecting the ability of *A. cristatellus* to spread to new areas. The transition from presence to absence of *A. cristatellus* coincides with an abrupt increase in impervious surface and a loss of forest habitat in some areas (see Fig. 2). The current distribution of *A. cristatellus* includes mostly higher-income neighborhoods including parts of Coconut Grove, Coral Gables, Pinecrest, and Key Biscayne (American Community Survey 2013; see also Ackley et al. 2015b). Socio-economic factors influence surface temperatures primarily through their impact on vegetation cover (Grove et al. 2006; Jenerette et al. 2007; Boone et al. 2010); such that areas with dense, mature tree canopies will produce relatively cooler microclimates suitable for *A. cristatellus*. These underlying effects of urban vegetation on available microclimates provide a mechanistic understanding of the current distribution of *A. cristatellus* in Miami. Other studies of urban and fragmented landscapes show species presence connected with other key resources, such as prey availability (e.g., Sullivan et al. 2014), shelter availability (e.g., Fischer et al. 2005), and structural habitat (e.g., Sarre et al. 1995; Garden et al. 2007; Santos et al. 2008) as well as urban development (e.g., Germaine and Wakeling 2001). Future studies should test whether socio-economic factors are correlated with vegetation and microclimates, and thus potentially useful for predicting the spread of *A. cristatellus* in Miami.

Thermal microclimates

We found substantial temperature differences between copper lizard models on open versus shaded trees (Fig. 3). Non-thermoregulating lizards would experience a temperature difference of up to a 7.6°C in the morning (1000 h) and a 5.7°C in the afternoon (1600 h). Open trees, but not shaded ones, experienced temperatures exceeding observed field T_b for *A. cristatellus* in the summer in Miami (Fig. 3). Denser overstory vegetation will produce relatively cooler microclimates favorable for *A. cristatellus* in the city. Shade from vegetation cooled buildings up to 11.7°C during summer conditions in Toronto, Canada (Millward et al. 2014), and shade from individual trees in city parks decreased average air temperatures by 10% and increased relative humidity by 18% in Thessaloniki, Greece (Georgi and Zafiriadis 2006). Ackley et al. (2015a), using copper lizard models, found that microclimates in areas with mesic landscaping were 5-10°C cooler than those in native xeric landscapes, even though the mean surface temperature of Phoenix, Arizona, USA was 3°C warmer than the surrounding desert. Interestingly, surface temperatures in Phoenix were related to vegetation during the daytime and the proportion of paved area during the night (Buyantuyev and Wu 2010). Daytime temperatures may limit activity or approach maximum thermal limits, whereas nighttime temperatures likely influence metabolic costs during times of inactivity. Whether the distribution of *A. cristatellus* in Miami is limited by daytime temperatures driven by vegetation, nighttime temperatures related to impervious surfaces, or both is a key question for future study.

Copper lizard model temperatures do not account for the ability of lizards to thermoregulate. If suitably cool microhabitats were nearby, lizards in open areas could behaviorally thermoregulate to preferred temperatures by shuttling between warm and cool spots, at the cost of increased movement rates. The cost of thermoregulation is predicted to be lower in more open sites because of the shorter distance to sunny patches, which lowers the energetic cost of shuttling between sun and shade (Huey 1974; Huey and Slatkin 1976; Huey and Webster 1976; Angilletta 2009). Accordingly, previous studies of *A. cristatellus* in Puerto Rico found that lizards actively thermoregulate in open habitats, but thermoconform in less variable, closed canopy habitats (Huey and Webster 1976). This versatility in thermoregulatory behavior suggests that *A. cristatellus* might occupy both open and closed canopy sites in Miami; however, *A. cristatellus* is generally restricted to relatively closed canopy locations (< 22% canopy openness; Fig. 4).

Our results suggest at least two possible explanations for this pattern. The first is that *A. cristatellus* uses relatively cooler microclimates strictly due to its thermal requirements: open canopy areas in Miami may be too warm relative to the preferred temperature and upper thermal limit of *A. cristatellus*, and thus not suitable for this species (Fig. 3). A second possibility is that *A. cristatellus* is excluded from warmer areas by the presence of *A. distichus* and *A. sagrei,* which both occupy warmer thermal niches than *A. cristatellus* (Huey and Webster 1976; Lee 1980; Gunderson and Leal 2012; Leal and Gunderson 2012; Kolbe et al. 2012, 2014; this study). The relative importance of these two factors on limiting the spread of *A. cristatellus* in the Miami area is an open question. These hypotheses need to be comprehensively evaluated by including sites where each species is present in the absence of the other as well as locations where they coexist. The importance of microclimates to competitive interactions between the species, allowing coexistence or contributing to competitive exclusion, warrants further investigation.

During the summer in Miami, shade from urban vegetation is expected to produce microclimates closer to the preferred body temperature of *A. cristatellus* as compared to more open areas (Fig. 3). Higher activity rates are predicted when lizards are closer to their preferred temperature (Gunderson and Leal 2015), allowing lizards to better forage, mate, defend their territories, and escape from predators. Mean body temperatures for *A. cristatellus* in Miami (28.8°C) and at low-elevation, mesic sites in Puerto Rico (~ 29°C from numerous sites; Huey and Webster 1976; Hertz 1992a,b; Gunderson and Leal 2012) were similar to preferred temperatures for lizards from three locations in Puerto Rico (range = 29.0-29.6°C; Huey and Webster 1976; Fig. 3). This suggests that some aspects of the thermal niche of *A. cristatellus* are conserved between introduced populations in South Miami and their low-elevation source population in northeast Puerto Rico (Kolbe et al. 2007). This similarity in field body temperatures occurs despite shifts in other aspects of their thermal niche, specifically the introduced population in South Miami rapidly acquired the ability to tolerate lower temperatures relative to its source population in Puerto Rico (see Kolbe et al. 2012; Leal and Gunderson 2012).

Effect of species interactions on the spread of A. cristatellus

Interspecific interactions, primarily competition, are thought to be important factors structuring both native and introduced *Anolis* lizard communities (Losos et al. 1993; Losos 2009). Previous experimental studies of anoles have found effects on abundance and structural habitat use consistent with interspecific competition when species coexist (e.g., Pacala and Roughgarden 1982; Rummel and Roughgarden 1985; Leal et al. 1998; Stuart et al. 2014). In accordance with predictions based on ecological similarity (primarily perch height), *A. cristatellus* presence showed the strongest negative association with *A. sagrei*, followed by *A. distichus*, and in a few cases with *A. carolinensis* and *A. equestris*. Thus, ecological similarity of interacting species may provide important information for predicting patterns of establishment and range expansion dynamics for introduced species.

The negative relationship between *A. cristatellus* and *A. sagrei* in Miami may be explained by resource competition and agonistic interference (Salzburg 1984, Losin 2012). When *A. cristatellus* was experimentally removed from plots five years after its initial introduction in 1981, *A. sagrei* rapidly shifted back to the structural habitat previously occupied by *A. cristatellus* — off the ground, on to trunks, and to shadier sites (Salzburg 1984). We found consistent patterns, with *A. cristatellus* occupying higher and broader perches as well as shadier microhabitats when sympatric with *A. sagrei*. Additionally, *A. cristatellus* was far less abundant when coexisting with congeners compared to when alone. However, competitive interactions between *A. cristatellus* and *A. sagrei* may have changed over time with their coexistence. Thirty years later, at the same site as Salzburg's experiment, another removal experiment did not influence habitat use or body condition of these two species (Losin 2012). Furthermore, *A. sagrei* lizards found sympatric with *A. cristatellus* were less aggressive toward this species compared to *A. sagrei* from allopartric populations (Losin 2012). Aggressive individuals facilitated the rapid range expansion of western bluebirds in the northwestern U.S., but following displacement of mountain bluebirds, their aggressive behavior decreased rapidly (Duckworth & Badyaev 2007). Given that *A. sagrei* is ubiquitous in Miami and *A. cristatellus* is still spreading, the opportunity exists to study resource use and aggression of *A. sagrei* before and after the arrival of *A. cristatellus.*

Summary

The occurrence of introduced *A. cristatellus* in Miami is strongly associated with forest habitat — dense vegetation, high canopy cover and low impervious surface — and the lack of congeners, particularly *A. sagrei*. Given the correlative nature of our analyses, it is difficult to tease apart the causal effects of urban vegetation and species interactions for limiting the spread of *A. cristatellus*. However, because *A. sagrei* already occupies nearly all habitats in Miami and forest habitat is highly fragmented across the city, we predict that dispersal to forest habitat will be the primary factor limiting future spread of *A. cristatellus*. Human-mediated, sometimes long-distance, dispersal is likely to contribute to spread as well as movement by diffusion through corridors of suitable habitats.

Acknowledgments

This research was supported by grants from the Harvard University Center for the Environment to RTTF and JBL, and the National Geographic Society, National Science Foundation (DEB-1354897) and University of Rhode Island Council for Research to JJK. We thank Rick Stanley for help in the field, Matthew Girard for producing maps of our study area, David Lee for assistance with tree identification, and Neil Losin and Nathan Dappen for logistical support in Miami.

Table 1. Variables recorded at each tree along transects designed to cross the distributional boundary of *A. cristatellus* in the Miami metropolitan area. Tree characteristics relate to the focal tree sampled and its surrounding vegetation. A total of 1035 trees were sampled on 19 transects in five plots. Congener presence refers to the four other species of *Anolis* lizards with distributions that overlap with *A. cristatellus* in Miami.

Variable	**Description**
Tree characteristics:	
Tree species	Species of tree
Native/non-native	Native or non-native tree species
Palm/non-palm	Palm or non-palm tree species
Trunk number	Number of trunks ≥ 10 cm at 1.35 m height; *Single, double, or multiple* (> 2 trunks)
Bark texture	*Overlapping* (overlapping protrusions covering the trunk, such as palms covered with the bases of dead leaf pedicles); *shallow furrows* (bark with furrows, gaps, or cracks ≥ 0.5 cm and no overlapping or flaking); *deep furrows* (bark separating or flaking ≥ 0.75 cm over an area ≥ 2x4 cm) or *smooth* (lacking any of the above characteristics)
Trunk diameter	Diameter (cm) of trunk at 1.35 m height
Canopy diameter	Mean canopy diameter (m) estimated from several measurements of the radius of the canopy
Distance to nearest plant	Distance (m) to the nearest stem at 1.35 m height
Distance to nearest tree	Distance (m) to the nearest tree with a diameter ≥ 30 cm at 1.35 m height
Overstory canopy cover	Mean percent overstory canopy cover both facing towards and away from the road as measured using a spherical densiometer
Congener presence:	
A. carolinensis	Presence/absence of *A. carolinensis*
A. distichus	Presence/absence of *A. distichus*
A. equestris	Presence/absence of *A. equestris*
A. sagrei	Presence/absence of *A. sagrei*

Table 2. GIS attributes derived from maps of forest fragmentation (NOAA 2010), percentage of human-made impervious surface (MRLC 2011), and variables recorded along transects.

GIS Attribute	Description
Block length	Length of each block in km
Trees per km	Number of trunks / Block length * 1000
Block canopy density	Number of trunks * Mean canopy diameter / Block length
Canopy cover GIS	Proportion of a 5-m buffer around the block transects including pixels classified as any type of forest
Distance to nearest forest	Distance (m) from each point to the center of the nearest pixel of any type of forest
Distance to nearest patch forest	Distance (m) from each point to the center of the nearest pixel of patch forest
Distance to nearest block forest	Distance (m) from each point to the center of the nearest pixel of non-patch forest (i.e., either perforated, edge or core forest)
Forest class	Indicates the type of forest for a point: 0 (no forest), 1 (patch), 2 (perforated/edge/core)
Impervious surface (1 pixel)	Value of the impervious raster pixel where each point is located (30m by 30m)
Impervious surface (9 pixels)	Average value of the 9 impervious raster pixels around each point (90m by 90m)
Impervious surface (25 pixels)	Average value of the 25 impervious raster pixels around each point (150m by 150m)

Table 3. Counts for the number of lizards present on surveyed trees (n=1035) and the percent of trees occupied by the five *Anolis* species encountered on transects in Miami. Results for each of three surveys are shown for A) all data, B) sections of transects where *A. cristatellus* is present, and C) sections of transects where *A. cristatellus* is absent. The combined surveys column indicates whether a species was present on a tree in at least one of the three surveys; these data were used in analyses.

A)	**1st survey Number of lizards**						**2nd survey Number of lizards**						**3rd survey Number of lizards**						**Combined surveys Number of lizards**		
Species	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**Absent**	**Present**	**%**
A. carolinensis	986	45	4	0	0	4.7	967	64	3	1	0	6.6	940	87	6	1	0	9.1	856	179	17.3
A. cristatellus	895	107	23	7	3	13.5	873	119	29	12	2	15.7	895	115	17	5	3	13.5	781	254	24.5
A. distichus	865	133	28	8	1	16.4	829	142	50	10	4	19.9	788	170	54	16	7	23.9	636	399	38.6
A. equestris	1029	6	0	0	0	0.6	1029	6	0	0	0	0.6	1013	6	0	0	0	0.6	1018	17	1.6
A. sagrei	838	135	43	10	9	19.0	812	157	47	8	11	21.5	831	142	36	11	14	19.6	660	375	36.2

B)	**1st survey Number of lizards**						**2nd survey Number of lizards**						**3rd survey Number of lizards**						**Combined surveys Number of lizards**		
Species	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**Absent**	**Present**	**%**
A. carolinensis	554	25	4	0	0	5.0	553	30	0	0	0	5.1	539	41	2	1	0	7.5	492	91	15.6
A. cristatellus	443	107	23	7	3	24.0	421	119	29	12	2	27.8	443	115	17	5	3	24.0	329	254	43.6
A. distichus	495	70	15	2	1	15.1	483	72	23	4	1	17.2	476	78	22	4	3	18.4	383	200	34.3
A. equestris	578	5	0	0	0	0.9	579	4	0	0	0	0.7	579	4	0	0	0	0.7	571	12	2.1
A. sagrei	492	66	17	3	5	15.6	496	61	16	4	6	14.9	512	51	11	4	5	12.2	428	155	26.6

C)	**1st survey Number of lizards**						**2nd survey Number of lizards**						**3rd survey Number of lizards**						**Combined surveys Number of lizards**		
Species	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**0**	**1**	**2**	**3**	**≥4**	**%**	**Absent**	**Present**	**%**
A. carolinensis	432	20	0	0	0	4.4	414	34	3	1	0	8.4	401	46	4	0	0	11.1	364	88	19.5
A. cristatellus																					0.0
A. distichus	370	63	13	6	0	18.1	346	70	27	6	3	23.5	311	92	32	12	4	31.0	253	199	44.0
A. equestris	451	1	0	0	0	0.2	450	2	0	0	0	0.4	434	2	0	0	0	0.5	447	5	1.1
A. sagrei	346	69	26	7	4	23.5	316	96	31	4	5	30.1	319	91	25	7	9	29.3	232	220	48.7

Table 4. Inferential statistics based on tree characteristics showing the most likely generalized linear models for presence-absence of *A. cristatellus* when A) dividing sections of transects into areas with *A. cristatellus* present versus absent (two groups), B) comparing the presence versus absence of *A. cristatellus* on all trees pooled, and C) comparing the presence versus absence of *A. cristatellus* on trees within only the sections of transects with *A. cristatellus* present, and for abundance of *A. cristatellus* for D) all trees pooled and E) within only the sections of transects with *A. cristatellus* present.

A)

Effect	**Effect df**	**Error df**	***Z***	***P***
Trunk diameter	1	1031	0.09	0.06
Canopy diameter	1	1030	0.13	0.16
Distance to nearest plant	1	1029	-0.53	< 0.0001
Overstory canopy cover	1	1028	0.41	< 0.0001

Note: second best model ΔAIC = 0.8; including the Distance to Nearest Tree effect; P=0.27.

B)

Effect	**Effect df**	**Error df**	***Z***	***P***
Canopy diameter	1	1031	0.27	< 0.001
Distance to nearest plant	1	1030	-0.86	< 0.0001
Distance to nearest tree	1	1029	-0.20	0.05
Overstory canopy cover	1	1028	0.90	< 0.0001

Note: second best model ΔAIC = 1.6; including the Trunk Diameter effect; P=0.53.

C)

Effect	**Effect df**	**Error df**	***Z***	***P***
Trunk diameter	1	580	0.51	< 0.0001
Distance to nearest plant	1	579	-0.87	< 0.0001
Overstory canopy cover	1	578	0.72	< 0.0001

Note: second best model ΔAIC = 1.37; including the Distance to Nearest Tree effect; P=0.43.

D)

Effect	**Effect df**	**Error df**	***Z***	***P***
Trunk diameter	1	1031	4.46	< 0.0001
Canopy diameter	1	1030	2.24	0.03
Distance to nearest plant	1	1029	-5.71	< 0.0001
Overstory canopy cover	1	1028	3.65	< 0.0001

Note: second best model ΔAIC=1.23; including the Distance to Nearest Tree effect; P=0.38.

E)

Effect	**Effect df**	**Error df**	***Z***	***P***
Trunk diameter	1	579	0.68	< 0.0001
Distance to nearest plant	1	580	-0.34	< 0.0001
Overstory canopy cover	1	578	0.32	< 0.0001

Note: second best model ΔAIC=1.59; including the Canopy Diameter effect; P=0.52.

Table 5. Inferential statistics for presence-absence of *A. cristatellus* showing the most likely generalized linear models when A) comparing street blocks with *A. cristatellus* present versus absent (n=93) and B) comparing the presence versus absence of *A. cristatellus* in 30 x 30 pixels (n=839). Selection of most favored models was supported by a likelihood ratio test against reduced models containing only the intercept term (A: χ^2 = 51.19, P <0.0001; B: χ^2 = 203.24, P <0.0001).

A)

Effect	**Effect df**	**Error df**	***Z***	***P***
Distance to nearest plant	1	92	-1.799	0.07
Mean overstory canopy cover	1	92	2.007	0.05
Trees per km	1	92	1.865	0.06
% Impervious-raster	1	92	-2.386	0.02

Note: second best model ΔAIC = 1.25; including the Distance to Nearest Tree effect; *P* = 0.39.

B)

Effect	**Effect df**	**Error df**	***Z***	***P***
Distance to nearest patch forest	1	838	8.752	< 0.0001
Distance to nearest block forest	1	838	-6.446	< 0.0001
Impervious surface (1 pixel)	1	838	-2.947	< 0.01
Impervious surface (25 pixels)	1	838	-4.318	< 0.0001

Note: second best model ΔAIC = 1.06; including the Forest_Class effect; *P* = 0.39.

Table 6. Results of likelihood ratio tests to determine whether the presence-absence of *A. cristatellus* on trees in Miami was related to the presence-absence of each of its four congeners. We combined trees on transects from each of the five plots analyzing A) all trees pooled and B) only trees from sections of transects with *A. cristatellus* present.

A)

		A. carolinensis		*A. distichus*		*A. sagrei*		*A. equestris*	
Plot	**N**	**X^2**	**P**	**X^2**	**P**	**X^2**	**P**	**X^2**	**P**
Charles	163	5.71	0.02	17.92	< 0.0001	18.90	< 0.0001	0.26	0.61
Le Jeune	125	0.25	0.61	0.27	0.60	4.21	0.04	7.32	< 0.01
Ludlum	270	0.59	0.44	1.32	0.25	7.81	< 0.01	0.03	0.86
Maynada	137	6.29	0.01	2.23	0.14	3.68	0.06	0.74	0.39
SW 104	340	0.56	0.45	0.85	0.36	28.91	< 0.0001	0.76	0.38
All Plots Combined	1035	2.38	0.12	7.21	< 0.01	59.19	< 0.0001	2.31	0.13

B)

		A. carolinensis		*A. distichus*		*A. sagrei*		*A. equestris*	
Plot	**N**	**X^2**	**P**	**X^2**	**P**	**X^2**	**P**	**X^2**	**P**
Charles	87	1.12	0.29	2.24	0.13	0.68	0.41	0.10	0.75
Le Jeune	80	0.42	0.52	0.13	0.72	1.95	0.16	4.60	0.03
Ludlum	215	0.00	0.99	0.39	0.53	7.52	< 0.01	0.04	0.85
Maynada	48	5.55	0.02	5.35	0.02	1.70	0.19	1.32	0.25
SW 104	153	0.20	0.65	0.53	0.47	3.34	0.07	2.77	0.10
All Plots Combined	583	0.71	0.40	1.58	0.21	22.23	< 0.0001	1.08	0.30

Figures Captions

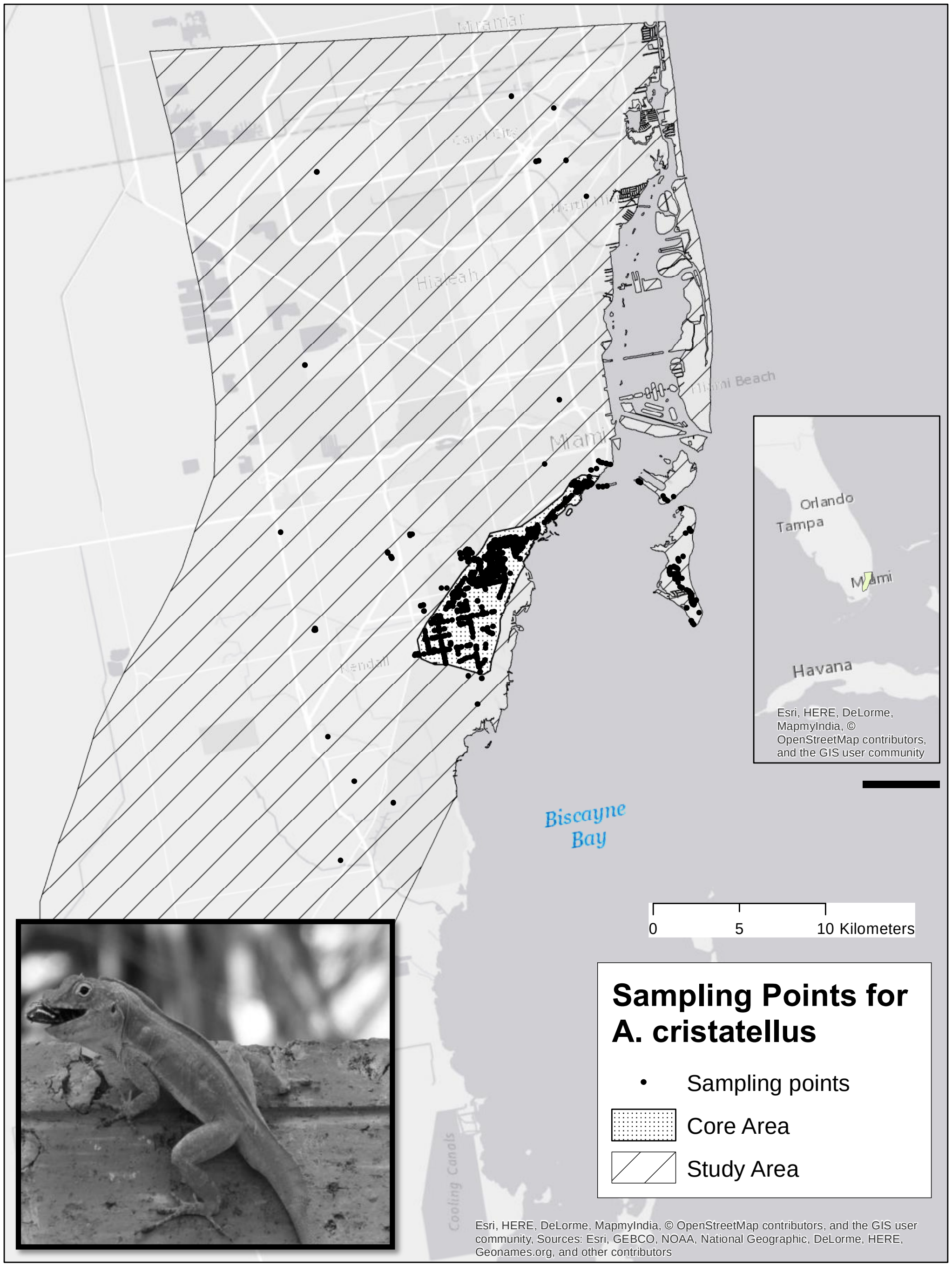
Fig. 1. Location of our study area in metropolitan Miami-Dade County of southeast Florida showing the core area in South Miami and sampling locations for *A. cristatellus*. Inset photo of a male *A. cristatellus* perched on a brick wall (J. Kolbe).

Fig. 2. Maps of a portion of the core area near Coconut Grove showing *A. cristatellus* presence and absence points and A) the four types of forest fragments and B) the percentage of impervious surface within 75 m.

Fig. 3. Mean temperatures for copper lizard models placed on the trunks of two trees, one with an open canopy and the other with a shaded canopy, in each cardinal direction. Points are hourly means collected over a 3.5-day period in July 2014 (error bars are omitted for clarity). Patterned shading (gray) shows the range of field T_b for *A. cristatellus* in Miami during each hour from 0800-1400 from this study as well as the preferred T_b (light gray) and the critical thermal maximum (dotted line) of *A. cristatellus* measured for populations from Puerto Rico (Huey and Webster 1976).

Fig. 4. Relationships between lizard field body temperature or copper lizard model temperature and significant covariates from the ANCOVA: a) canopy openness, b) air temperature, and c) time of day for *A. cristatellus* (black circles), *A. sagrei* (white circles), and copper lizard models at random locations (gray circles) in South Miami. Separate slopes are shown for the significant temperature by canopy openness interaction.

Fig. 1.

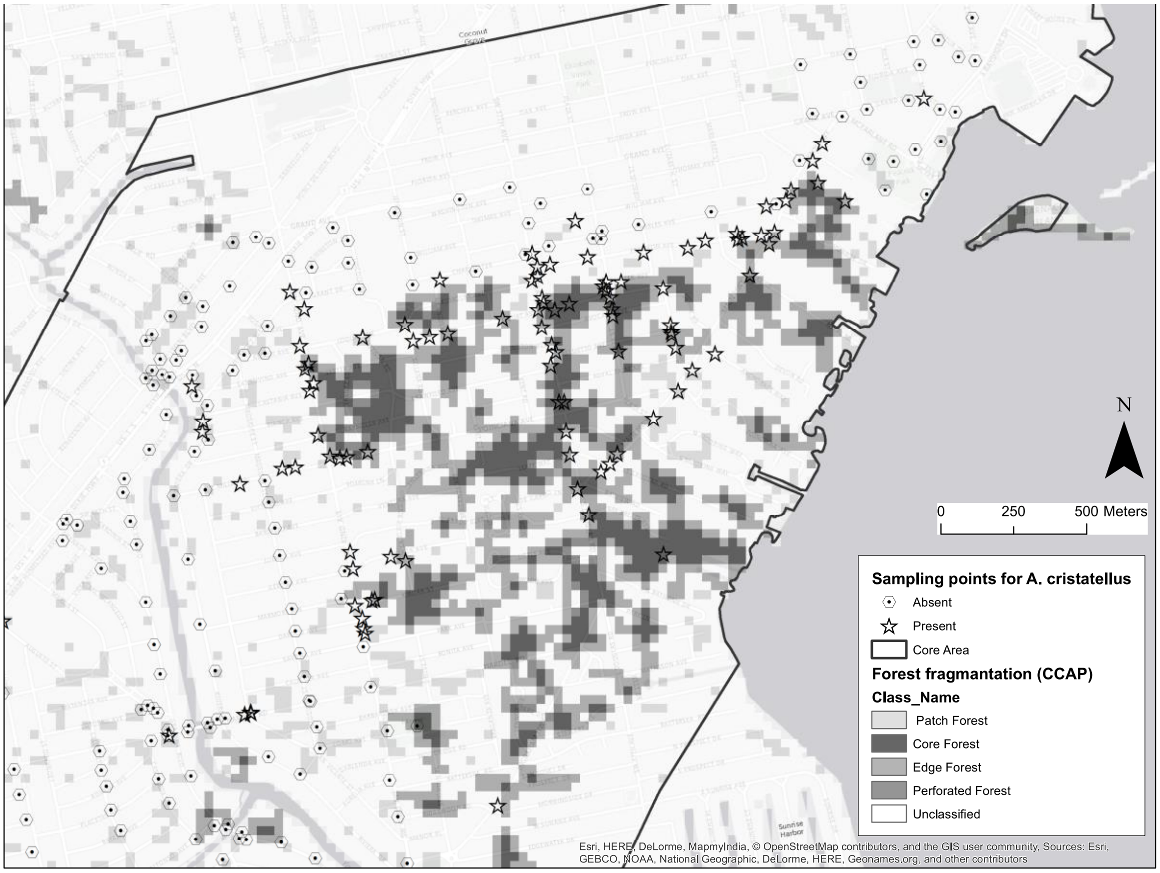


Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community, Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

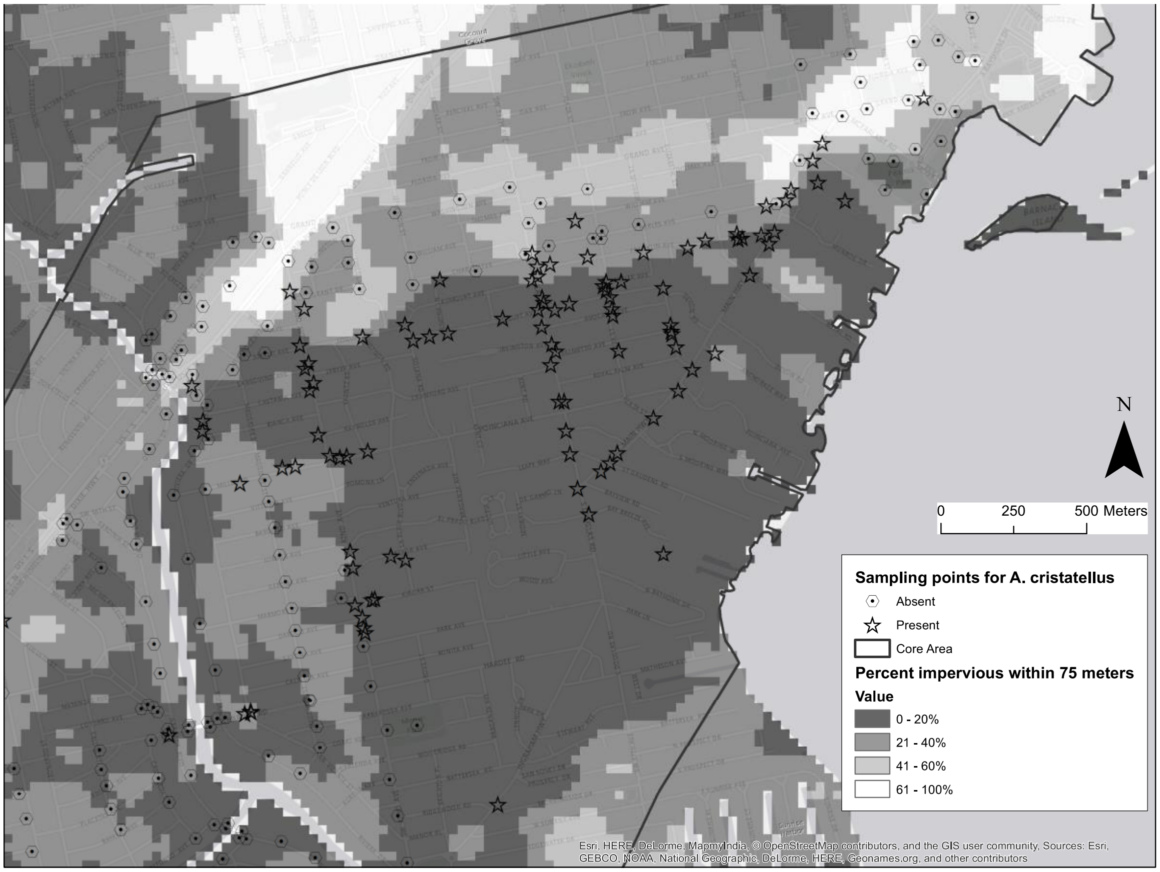
Fig. 2.

A)



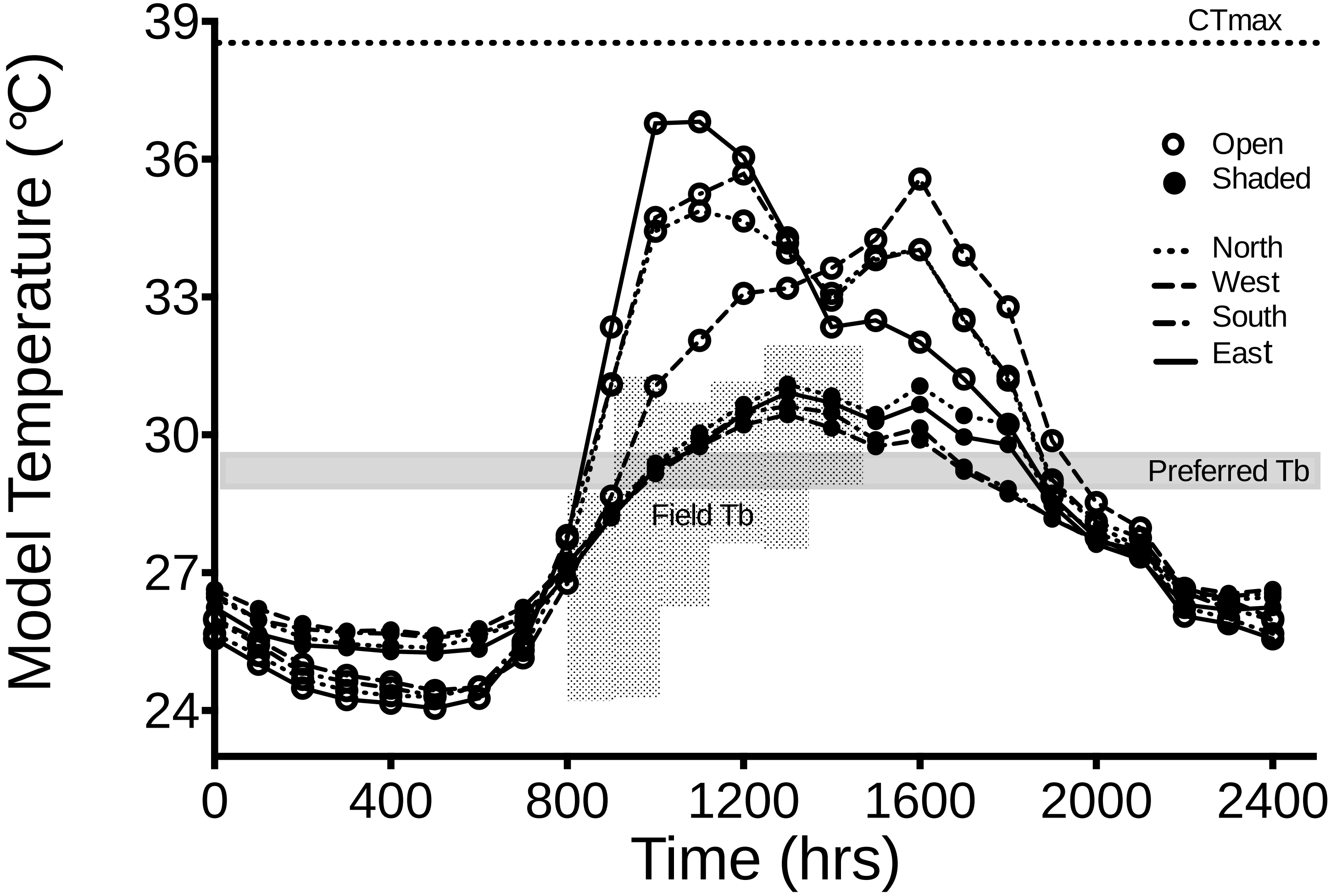
Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community, Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

B)



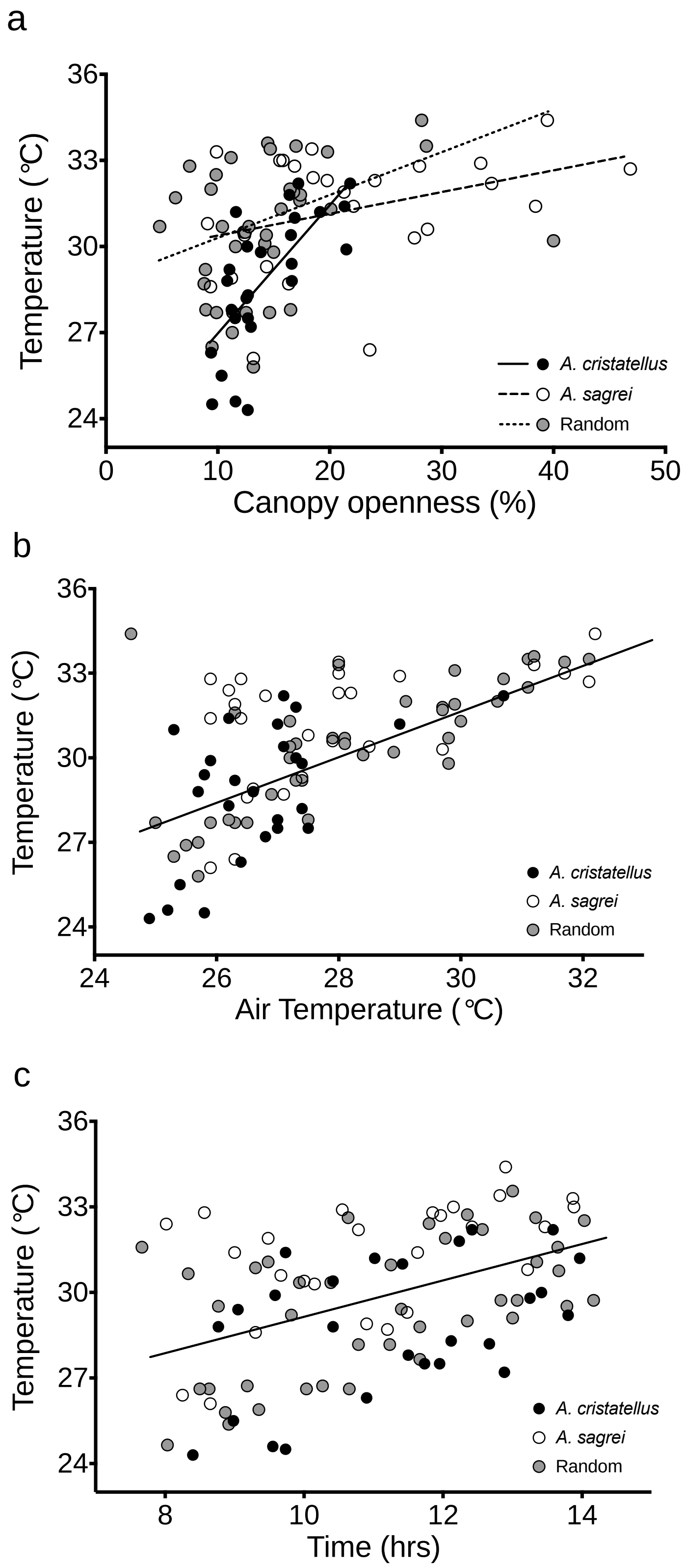
Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community, Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

Fig. 3.



CTmax
39
36
33
30
27
24
Model Temperature (°C)
○ Open
● Shaded
North
West
South
East
Preferred Tb
Field Tb
0
400
800
1200
1600
2000
2400
Time (hrs)

Fig. 4.


a
Temperature (℃)
36
33
30
27
24
0
10
20
30
40
50
Canopy openness (%)
A. cristatellus
A. sagrei
Random
b
Temperature (℃)
36
33
30
27
24
24
26
28
30
32
Air Temperature (℃)
A. cristatellus
A. sagrei
Random
c
Temperature (℃)
36
33
30
27
24
8
10
12
14
Time (hrs)
A. cristatellus
A. sagrei
Random

References

Ackley JW, Angilletta MJ Jr., DeNardo D, Sullivan B, Wu J (2015a) Urban heat island mitigation strategies and lizard thermal ecology: landscaping can quadruple potential activity time in an arid city. Urban Ecosyst DOI 10.1007/s11252-015-0460-x.

Ackley JW, Wu J, Angilletta MJ Jr., Myint SW, Sullivan B (2015b) Rich lizards: how affluence and land cover influence the diversity and abundance of desert reptiles persisting in an urban landscape. Biol Conserv 182:87-92.

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Akbari H, Pomerantz M, Taha H (2001) Cool surfaces and shade trees to reduce energy use and improve air quality in urban areas. Solar Energy 70:295-310.

American Community Survey (2013) United States Census Bureau. Available from http://www.census.gov (accessed August 2015)

Anderson L, Burgin S (2008) Patterns of bird predation on reptiles in small woodland remnant edges in peri-urban north-western Sydney, Australia. Landscape Ecol 23:1039-1047.

Angilletta MJ Jr (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Arnfield AJ (2003) Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. Int J Climatol 23:1-26.

Bartlett RD, Bartlett PP (1999) A field guide to Florida reptiles and amphibians. Gulf Publishing, Houston.

Bonnington C, Gaston KJ, Evans KL (2014) Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. Urban Ecosyst 17:533-546.

Boone CG, Cadenasso ML, Grove JM, Schwarz K, Buckley GL (2010) Landscape, vegetation characteristics, and group identity in an urban and suburban watershed: why the 60s matter. Urban Ecosyst 13:255-271.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M-J, Randin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecol Biogeo 21:481–497.

Buyantuyev A, Wu J (2010) Urban heat islands and landscape heterogeneity: linking spatiotemporal variations in surface temperatures to land-cover and socioeconomic patterns. Landscape Ecol 25:17-33.

Cadenasso ML, Pickett STA, Schwarz K (2007) Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. Front Ecol Environ 5:80-88.

Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the Tropical Pacific. Ecology 75:464-477.

Chen WY, Jim CY (2008) Assessment and valuation of the ecosystem services provided by urban forests. In: Ecology, planning, and management of urban forests international perspective. Springer, New York, pp 53–83.

Corn MJ (1971) Upper thermal limits and thermal preferenda for three sympatric species of *Anolis.* J Herpetol 5:17-21.

Crump ML, Scott NJ Jr (1994) Visual encounter surveys, p. 84–92. In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. A. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.

Davis MA (2009) *Invasion Biology*. Oxford University Press.

Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilities the rapid range expansion of a passerine bird. PNAS 104:15017-15022.

Forman RTT (2014) *Urban Ecology*. Cambridge University Press.

Fischer J, Lindenmayer DB, Barry S, Flowers E (2005) Lizard distribution patterns in the Tumut fragmentation "Natural Experiment" in south-eastern Australia. Biol Conserv 123:301-315.

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Garden JG, McAlpine CA, Possingham HP, Jones DN (2007) Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: a case study from Brisbane, Australia. Austral Ecol 32:669-685.

Georgi NJ, Zafiriadis K (2006) The impact of park trees on microclimate in urban areas. Urban Ecosyst 9:195-209.

Germaine SS, Wakeling BF (2001) Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol Conserv 97:229-237.

Grove JM, Troy AR, O'Neil-Dunne JPM, Burch WR, Cadenasso ML, Pickett STA (2006) Characterization of households and its implications for the vegetation of urban ecosystems. Ecosystems 9:578-597.

Gunderson AR, Leal M (2012) Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. Funct Ecol 26:783-793.

Gunderson AR, Leal M (2015) Patterns of thermal constraint on ectotherm activity. Am Nat 185: In press.

Hamdi R, Schayes G (2008) Sensitivity study of the urban heat island intensity to urban characteristics. Int J Climatol 28:973-982.

Hines JE (2006) PRESENCE - Software to estimate patch occupancy and related parameters. USGS-PWRC http://www.mbr-pwrc.usgs.gov/software/presence.html.

Huang L, Li J, Zhao D, Ahu J (2008) A fieldwork study on the diurnal changes of urban microclimate in four types of ground cover and urban heat island of Nanjing, China. Building and Environ 43:7-17.

Hertz PE (1992) Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. Ecology 73:1405–1417.

Huey RB (1974) Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001–1003.

Huey RB, Webster TP (1976) Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group on Puerto Rico. Ecology 57:985–994.

Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. Quart Rev Biol 51:363-384.

Irschick DJ, Carlisle E, Elstrott J, Ramos M, Buckley C, Vanhooydonck B, Meyers J, Herrell A (2005) A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. Biol J Linnean Soc 85:223-234.

Jenerette GD, Harlan SL, Brazel A, Jones N, Larsen L, Stefanov WL (2007) Regional relationships between surface temperature, vegetation, and human settlement in a rapidly urbanizing ecosystem. Landscape Ecol 22:353-365.

Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB (2007) Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. Conserv Biol 21:1612-1625.

Kolbe JJ, Colbert PL, Smith BE (2008) Niche relationships and interspecific interactions in Antiguan lizard communities. Copeia 2008:261-272.

Kolbe JJ, VanMiddlesworth PS, Losin N, Dappen N, Losos JB (2012) Climatic niche shift predicts thermal trait response in one but not both introductions of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, USA. Ecol Evol 2: 1503-1516.

Kolbe JJ, Ehrenberger JC, Moniz HA, Angilletta MJ (2014) Physiological Variation among Invasive Populations of the Brown Anole (*Anolis sagrei*). Physiol Biochem Zool 87:92-104.

Kolbe JJ, Battles AC, Avilés-Rodríguez KJ (2015) City slickers: poor performance does not deter *Anolis* lizards from using artificial substrates in human-modified habitats. Funct Ecol doi: 10.1111/1365-2435.12607

Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer.

Leal M, Gunderson AR (2012) Rapid change in the thermal tolerance of a tropical lizard. Am Nat 180:815-822.

Leal M, Rodríguez-Robles JA, Losos JB (1998) An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. Oecologia 117:273-278.

Lee JC (1980) Comparative thermal ecology of two lizards. Oecologia 44:171-176.

Lever C (2003) *Naturalized reptiles and amphibians of the world.* Oxford University Press.

Liu X, Li X, Liu Z, Tingley R, Kraus F, Guo Z, Li Y (2014) Congener diversity, topographic heterogeneity and human-assisted dispersal predict spread rates of alien herpetofauna at a global scale. Ecol Lett 17:821-829.

Lockwood JL, Hoopes MF, Marchetti MP (2007) *Invasion Ecology*. Blackwell Publishing.

Losin NJE (2012) The evolution and ecology of interspecific territoriality: studies of *Anolis* lizards and North American wood-warblers. Dissertation. University of California Los Angeles.

Losos JB (1994) Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Ann Rev Ecol Syst 25:467-493.

Losos JB (2009) *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley.

Losos JB, Marks JC, Schoener TW (1993) Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman. Oecologia 95:525-532.

Luck GW, Smallbone LT, O'Brien R (2009) Socio-economics and vegetation change in urban ecosystems: patterns in space and time. Ecosystems 12:604-620.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Marnocha E, Pollinger J, Smith TB (2011) Human-induced morphological shifts in an island lizard. Evol Appl 4:388-396.

Martin CA, Warren PS, Kinzig AP (2004) Neighborhood socioeconomic status is a usefull predictor of perennial landscape vegetation in residential neighborhoods and embedded small parks of Phoenix, AZ. Landscape Urban Plan 69:355-368.

McCullagh P, Nelder J (1989) Generalized linear models, 2nd ed. Chapman and Hall/CRC, Boca Raton.

Millward AA, Torchia M, Laursen AE, Rothman LD (2014) Vegetation placement for summer built surface temperature moderation in an urban microclimate. Environ Man 53:1043-1057.

Multi-resolution land characteristics (MRLC) consortium (2011) The national land cover database: percent developed imperviousness. Available from http://www.mrlc.gov

National Oceanic and Atmospheric Administration (NOAA) Office for Coastal Management (2010) Coastal Change Analysis Program (C-CAP) Regional Land Cover Database. Available from http://www.coast.noaa.gov/dataregistry/search/dataset/info/forestfrag

Nowak DJ, Rowntree RA, McPherson EG, Sisinni SM, Kerkmann ER, Stevens JC (1996) Measuring and analyzing urban tree cover. Landscape Urban Plan 36:49-57.

Pacala S, Roughgarden J (1982) Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444-446.

Perry G, Buchanan BW, Fisher RN, Salmon M, Wise SE (2008) Effects of artificial night lighting on amphibians and reptiles in urban environments. In *Urban Herpetology* (Mitchell JC, Jung Brown RE, Bartholomew B, eds). Society for the Study of Amphibians and Reptiles, pp. 239-256.

Petren K, Case TJ (1996) An experimental demonstration of exploitation competition in an ongoing invasion. Ecology 77:118-132.

Pianka ER (1981) Competition and niche theory. In *Theoretical Ecology* (May RM, ed). Blackwell, pp 167-196.

Pickett STA, Cadenasso ML Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R (2001) Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annu Rev Ecol Syst 32:127-157.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/

Ramalho CE, Hobbs RJ (2011) Time for a change: dynamic urban ecology. Trends Ecol Evol 27:179-188.

Rizwan AM, Dennis YCL, Liu C (2008) A review of the generation, determination and mitigation of Urban Heat Island. J Environ Sci 20:120-128.

Royle JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.

Rummel J, Roughgarden J (1985) Effects of reduced perch-height separation on competition between two *Anolis* lizards. Ecology 66:430-444.

Salzburg MA (1984) *Anolis sagrei* and *Anolis cristatellus* in Southern Florida: a case study in interspecific competition. Ecology 65:14-19.

Santos T, Diaz JA, Perez-Tris J, Carbonell R, Tellera JL (2008) Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. Animal Conserv 11:46-56.

Sarre S, Smith GT, Meyers JA (1995) Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. Biol Conserv 71:25-33.

Schwartz A, Thomas R (1975) A checklist of West Indian amphibians and reptiles. Special Publication. Carnegie Museum of Natural History 1:1-216.

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006). From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186-191.

Stuart YE, Campbell TS, Hohenlohe PA, Reynolds RG, Revell LJ, Losos JB (2014) Rapid evolution of a native species following invasion by a congener. Science 346: 463-466.

Sullivan BK, Sullivan KO, Vardukyan D, Suminski T (2014) Persistence of Horned Lizards (*Phrynosoma* spp.) in urban preserves of Central Arizona. Urban Ecosyst 17:707-717.

White CR (2003) Allometric analysis beyond heterogeneous regression slopes: use of the Johnson-Neyman technique in comparative biology. Physiol Biochem Zool 76:135-140.

Wilson LD, Porras L (1983) The ecological impact of man on the south Florida herpetofauna. University of Kansas Museum of Natural History Special Publication No. 9:1-89.

Wong NH, Yu C (2005) Study of green areas and urban heat island in a tropical city. Habitat International 29:547-558.

Supplementary Table 1. Estimates of detection probability calculated from single-season presence-absence occupancy models using sampling covariates of each surveyor and all surveyors combined. Models were built using three repeat surveys of 38 independent sampling points. Mean values are shown with 1 SE in parentheses. No variation exists for PV detection probabilities because this surveyor was present for each sampling event. Low detection probabilities for *A. equestris* likely reflect the low numbers observed for this species (Table 3). Estimates of detection probabilities for the three most common species were sufficiently high (> 0.87) to consider detection unlikely to influence subsequent analyses of presence-absence and abundance.

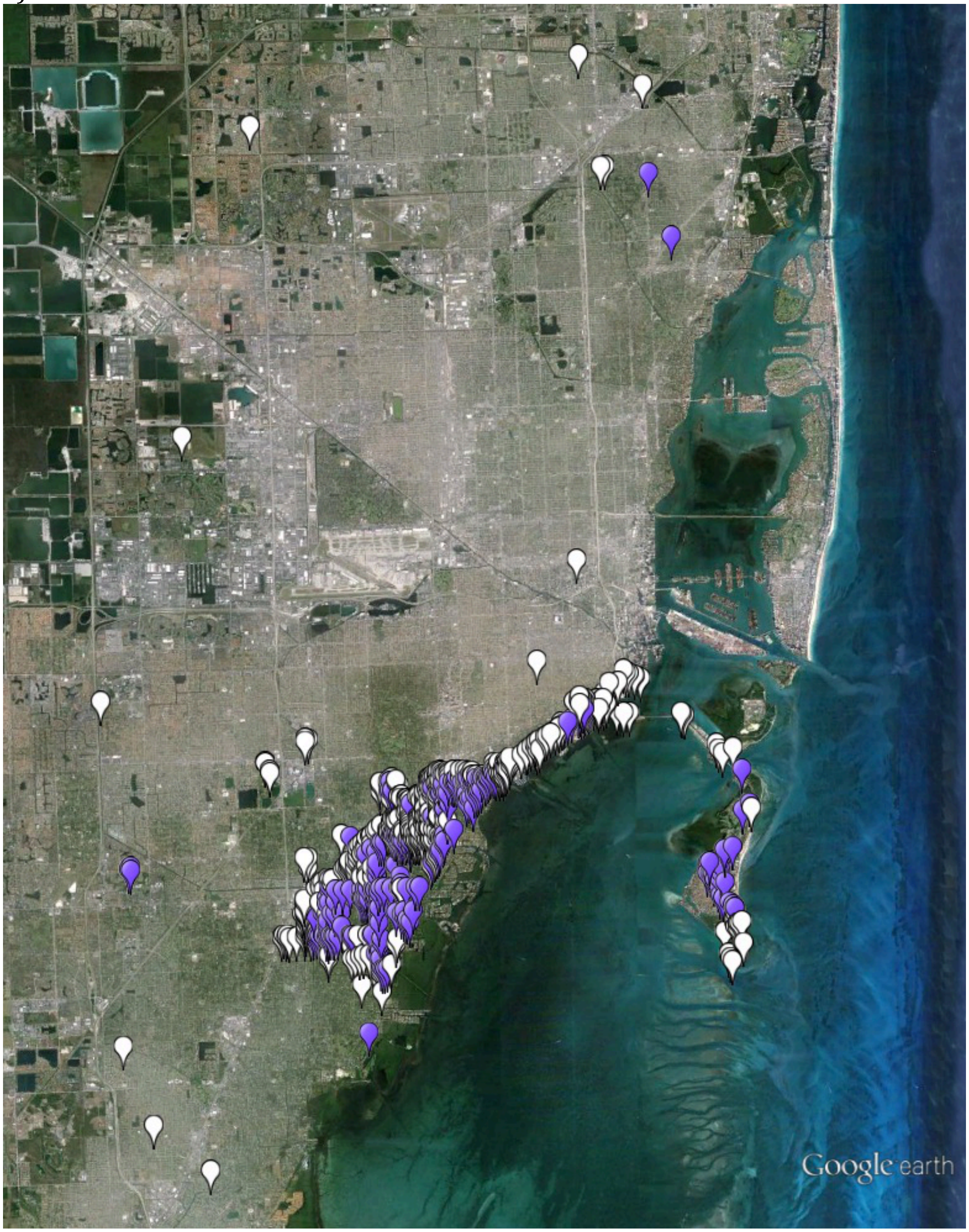
	Model			
Species	**psi(.),p(JJK)**	**psi(.),p(PV)**	**psi(.),p(RS)**	**psi(.),p(All Surveyors)**
A. cristatellus	0.9003	0.6340	0.7781	0.8807
	(0.039)	(0.000)	(0.035)	(0.020)
A. sagrei	0.7368	0.9298	0.5921	0.9298
	(0.033)	(0.000)	(0.024)	(0.012)
A. distichus	0.7018	0.8772	0.6097	0.8772
	(0.028)	(0.000)	(0.028)	(0.006)
A. carolinensis	0.6524	0.7240	0.5766	0.7302
	(0.021)	(0.000)	(0.020)	(0.010)
A. equestris	0.4021	0.2323	0.4479	0.2056
	(0.014)	(0.000)	(0.013)	(0.009)

Supplementary Table 2. Proportion of forest fragmentation using previously defined forest categories and impervious surface cover using two spatial scales for the study area and core area in the Miami.

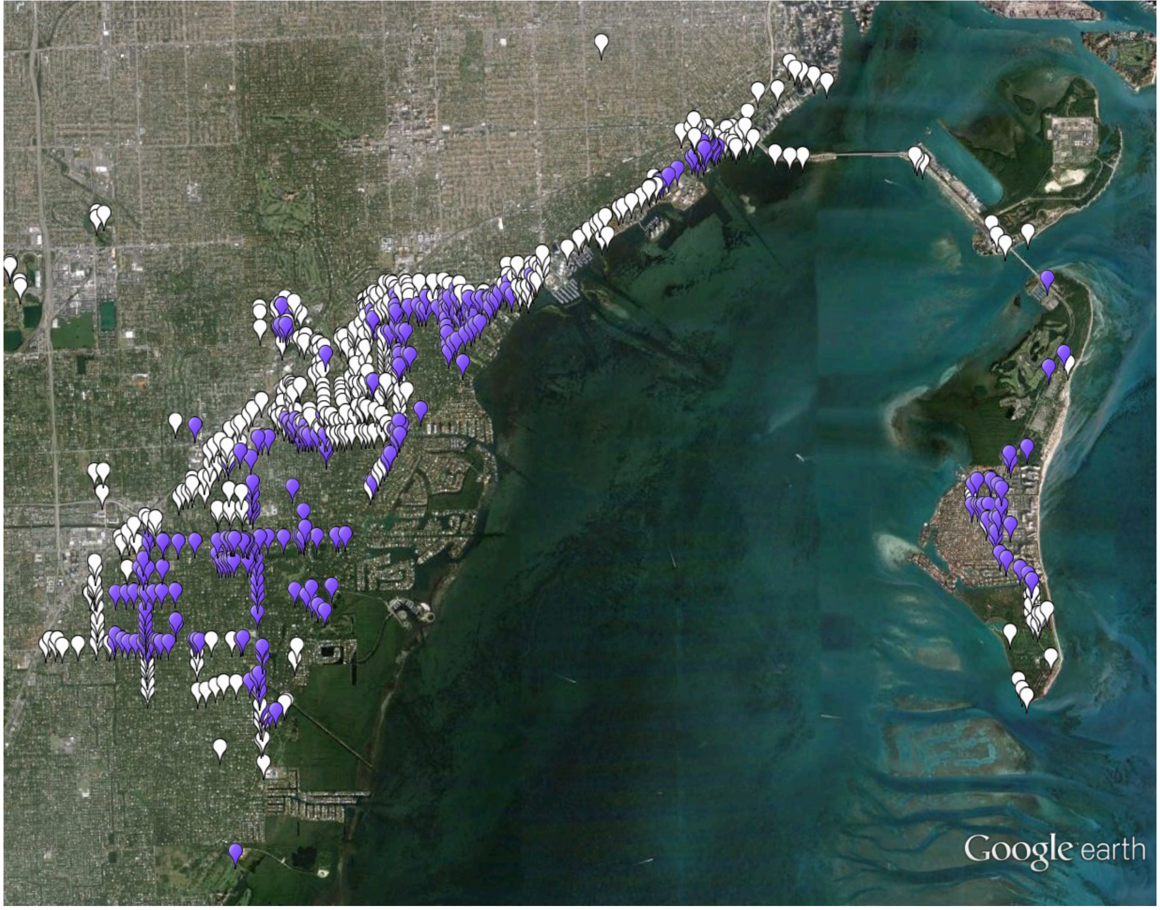
Attribute	**Category**	**Proportion of Study Area (1,511 km^2)**	**Proportion of Core Area (33.63 km^2)**
Forest fragmentation	Core Forest	0.02	0.06
	Patch Forest	0.03	0.06
	Perforated Forest	0.00	0.01
	Edge Forest	0.03	0.13
	Non-forest	0.92	0.73
Impervious surface cover (within 15m)	0-20%	0.43	0.59
	21-40%	0.27	0.28
	41-60%	0.18	0.08
	61-100%	0.13	0.06
Impervious surface cover (within 75m)	0-20%	0.47	0.57
	21-40%	0.20	0.26
	41-60%	0.16	0.09
	61-100%	0.17	0.08

Supplementary Fig. 1. The distribution of *A. cristatellus* in the Miami metropolitan area showing presence (purple) and absence (white) points for a) the entire area surveyed including regional waste transfer stations and municipal parks and b) a view of the core distribution in South Miami and Key Biscayne (see attached .kmz file).

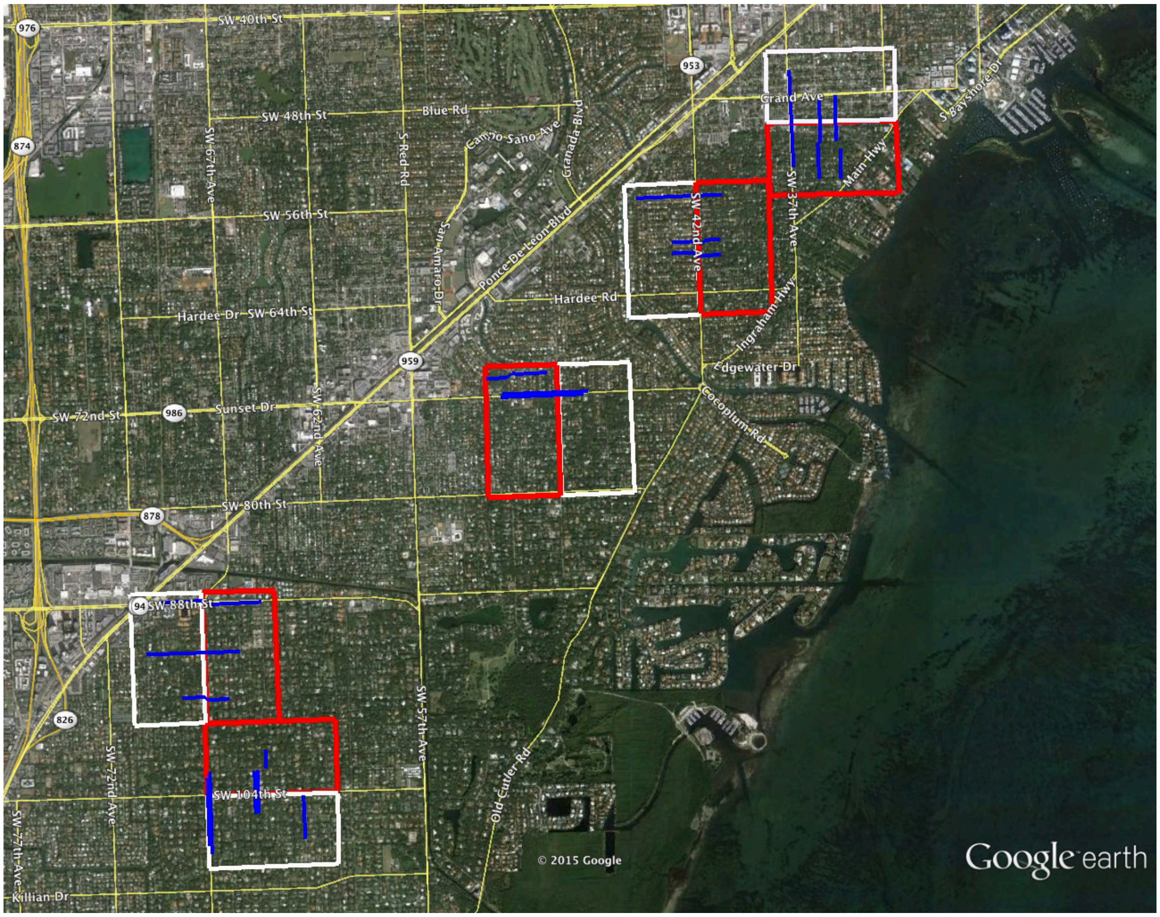
a)



b)

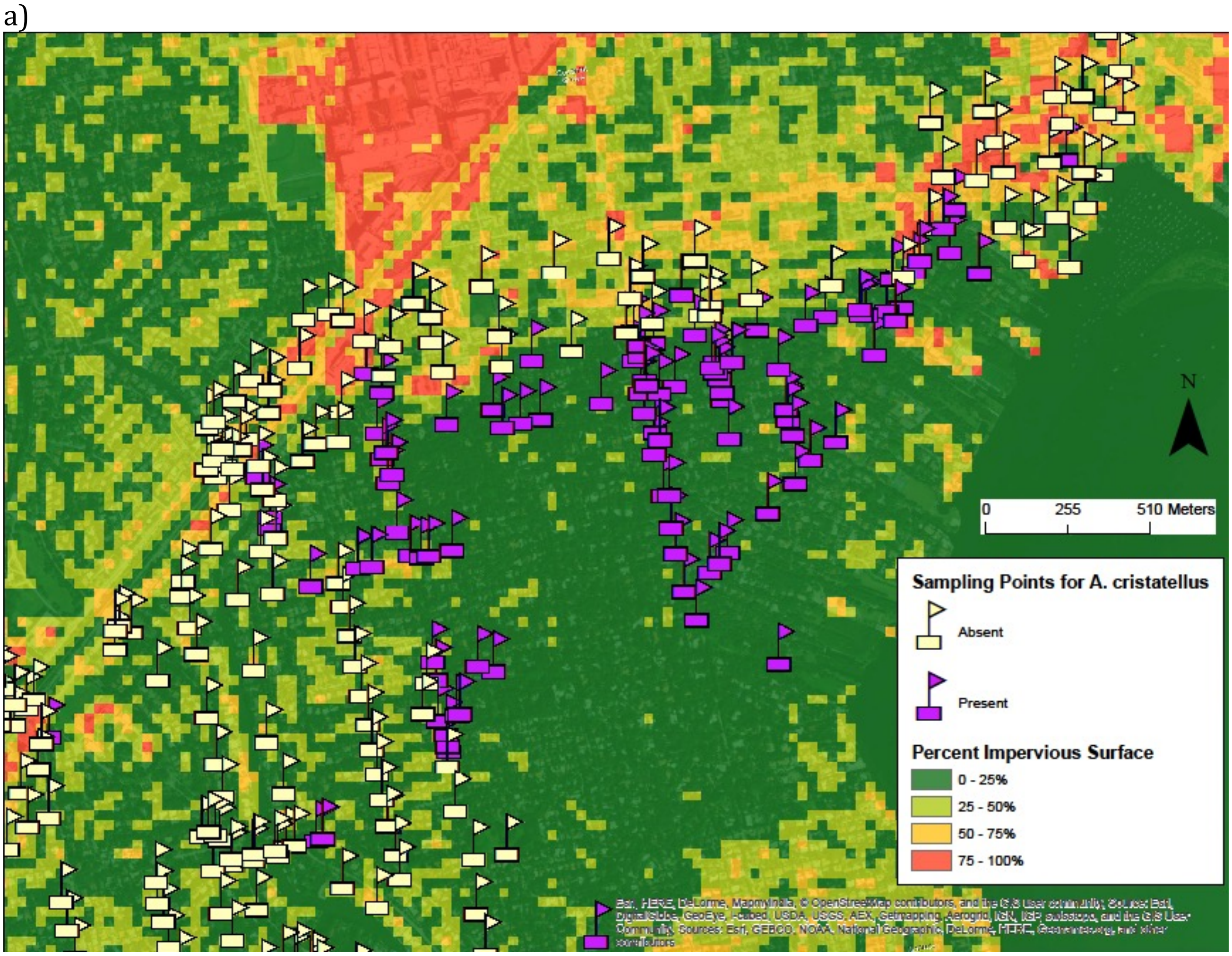


Supplementary Fig. 2. Map showing the location of the five plots and 19 transects in South Miami used to survey for the presence of *A. cristatellus*. We established plots crossing observed transitions from presence (red rectangles) to absence (white rectangles) of *A. cristatellus* based on preliminary surveys. In each plot, we established three to six roadside transects (blue lines) running perpendicular to the transition zone.



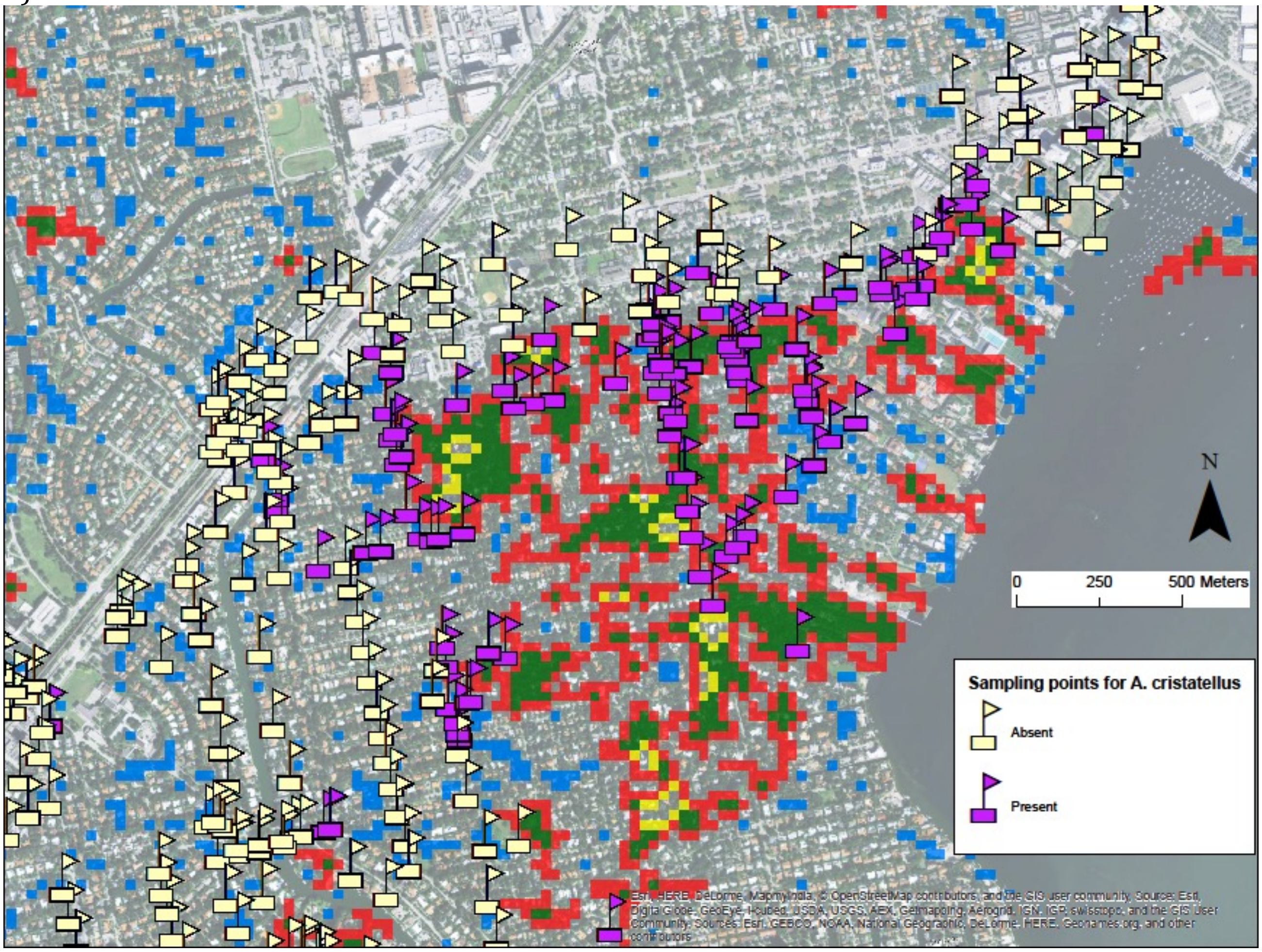
Supplementary Figure 3. GIS-based map for a portion of the distribution of *A. cristatellus* in Coconut Grove showing presence and absence points and a) percentage of impervious surface divided into four categories and b) the four forest fragmentation types. This is a color version of Fig. 2.

a)



Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS User community; Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

b)



Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community. Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

Supplementary Figure 4. Overstory canopy photos facing in the four cardinal directions for representative a) shaded and b) open canopy trees. Percentage of overstory cover is shown next to each photo.