Science of the Total Environment 711 (2020) 135133

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Stormwater ponds: An overlooked but plentiful urban designer ecosystem provides invasive plant habitat in a subtropical region (Florida, USA)

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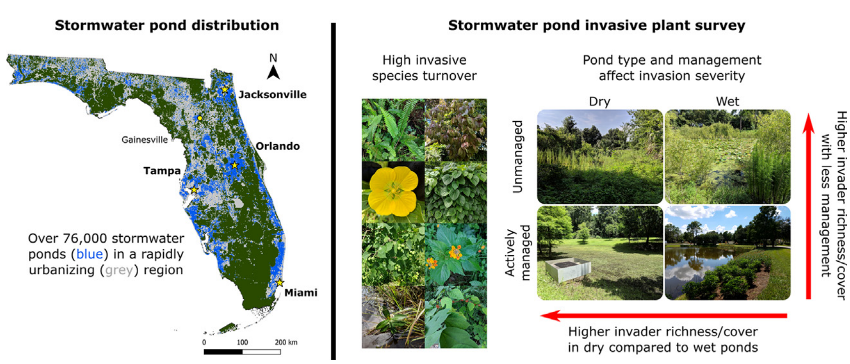
HIGHLIGHTS

- Urban stormwater ponds used to manage runoff could facilitate plant invasion.
- We identified over 76,000 stormwater ponds across Florida, US.
- Ponds in Gainesville, FL harbor high richness and cover of invasive plants.
- Invasion severity is highest in temporary ponds with little to no management.
- Results highlight the commonality and disservices of these designed ecosystems.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 20 August 2019
Received in revised form 19 October 2019
Accepted 21 October 2019
Available online 22 November 2019

Keywords:
Urban
Invasion
Stormwater pond
Designed ecosystem
Invasive plant
Ecosystem disservices

ABSTRACT

Designed ecosystems are built as part of ongoing urban expansion, providing a suite of valued ecosystem services. However, these new ecosystems could also promote disservices by facilitating the colonization and spread of invasive species. We conduct the first assessment of the quantity and invasion of an overlooked designed ecosystem: stormwater ponds. These ponds are commonly recommended for managing urban hydrology, but little is known about their ecology or extent of proliferation. Using a broad-scale survey of pond coverage in Florida, USA, we found that over 76,000 stormwater ponds have been built just in this state, forming 2.7% of total urban land cover. This extensive pondscape of manufactured habitats could facilitate species spread throughout urban areas and into nearby natural waterbodies. We also conducted a survey of the severity of plant invasion in 30 ponds in Gainesville, FL, US across two pond types (dry vs. wet), and a gradient of management intensities (low, medium, high) and pond ages. We unexpectedly found a high number of invasive plant species (28 in just 30 ponds). Ninety-six percent of surveyed ponds contained from one to ten of these species, with ponds exhibiting high turnover in invader composition (i.e., high beta diversity). The bank sections of dry unmanaged ponds exhibited the highest mean invasive species richness (5.8 ± 1.3) and the inundated centers of wet medium managed ponds exhibited the highest mean invasive species cover (34 ± 12%). Invasive plant richness and cover also tended to be greater in dry ponds with higher soil nutrient levels, and in older wet ponds. Therefore, we found that highly maintained and younger wet ponds were the least invaded.

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https://doi.org/10.1016/j.scitotenv.2019.135133

Nevertheless, common management practices that limit plant invasions may also limit native species establishment and invasion may increase in the decades following pond construction.

1. Introduction

Urbanization drives the construction of new, anthropogenic habitats, such as gardens, parks, lawns and engineered waterbodies. These 'designed ecosystems' (synthetic systems created to achieve ecological, social and/or economic goals; sensu Palmer et al., 2004), and the ecological communities they harbor, can replace some of the ecological functioning lost to urban expansion (Goddard et al., 2010; Andersson et al., 2014; Hassall, 2014). However, while the positive services provided by urban ecosystems are increasingly studied, we have a poor understanding of their associated disservices (Lyytimäki and Sipilä, 2009; Oertli and Parris, 2019). Of particular concern is how designed ecosystems may facilitate biological invasions, which inflict economic and ecological damage across the globe (Pimentel, 2014). Urban centers are foci for invasive species (Gaertner et al., 2017) and designed ecosystems are colonizable, nutrient-rich, disturbed habitats that could subsequently promote invader establishment and facilitate the spread of invaders across urban landscapes (McKinney, 2008; Potgieter et al., 2017; Oertli and Parris, 2019).

Species invasions have been studied more extensively in some types of designed ecosystems, notably gardens (e.g., Bigirimana et al., 2012; Padullés Cubino et al., 2015). However, the role of other potentially common urban designed ecosystems in facilitating invasion has been largely ignored. Of particular importance to the function of urban areas are small waterbodies built as part of recommended 'Best Management Practice' (BMP; e.g., US: National Research Council (NRC), 2009; Europe: Revitt et al., 2003; Australia: Department of Water, 2007) to attenuate and store runoff from impervious surfaces (hereafter referred to as 'stormwater ponds'). These ponds encourage pollutant removal and reduce downstream flooding risk and erosion in receiving natural waters; Paul and Meyer, 2001; Tixier et al., 2011). Stormwater ponds and other engineered ecosystems have thus largely replaced natural systems (e.g., headwater streams or riparian zones; Bettez and Groffman, 2012; Kaushal and Belt, 2012) as the primary interface responsible for mitigating the impacts of urbanized landscapes on surrounding waterbodies. Additionally, natural ponds are generally declining in quantity and quality across the globe (Vörösmarty et al., 2010) while the quantity of new, artificial ponds is increasing (e.g., Biggs et al., 2005). Manufactured ponds therefore have a key role to play in protecting urban-associated waterbodies and providing some of the ecological services in urban landscapes that are lost when natural waterbodies are degraded, removed or replaced, such as by improving the biodiversity of urban plants, amphibians and invertebrates (Scher et al., 2004; Le Viol et al., 2012; Hassall and Anderson, 2015).

Despite the likely widespread utilization of stormwater ponds in urban watersheds, and the valuable ecological services they can provide, we do not know how often these ponds serve a negative ecological function as habitat for invasive species, especially plants. While the potential for stormwater ponds to facilitate invasions has been mentioned (e.g., McCarthy and Lathrop, 2011), there is almost no research that specifically addresses this question (but see Kwik et al., 2013). Stormwater ponds are often purposefully planted with or naturally colonized by a variety of plants and possess a unique set of characteristics that could promote plant invasion. Pond occurrence spatially coincides with areas of intense human activity, which is a source of disturbance and a frequent driver of plant invasion (Sher and Hyatt, 1999; Riitters et al., 2018). Stormwater ponds also collect water and nutrients, thus likely receiving propagules and resources that facilitate plant establishment. Furthermore, urban pond hydrology is highly variable due to the 'flashy' hydrology of urban watersheds (Paul and Meyer, 2001; Kaushal and Belt, 2012). Such dynamic, disturbed habitats can experience greater fluctuations in species abundance and resource availability, creating windows of opportunity for plant colonists (Davis et al., 2000). To summarize, the urbanization-driven proliferation of stormwater ponds is disseminating colonizable habitats that may promote species introduction and establishment, attributes which are common ingredients in the ideal recipe for biological invasions (Catford et al., 2009). Stormwater ponds are also integrated into city stormwater management networks that often drain into natural waterbodies. Any invasive plant or other ecological disservice facilitated by urban stormwater ponds could therefore impact both other city ecosystems and nearby aquatic habitat (Vincent and Kirkwood, 2014).

Further complicating the stormwater pond-invasion issue is that the composition and severity of plant invasion likely depends upon the context of the ecosystem. Cities vary in their climate, history of development and pool of introduced species (Kowarik, 2011; Aronson et al., 2016), all of which could affect urban invasions. This cross-city variability necessitates the continued investigation of individual urban areas. Stormwater ponds can also be designed differently, with some built to completely drain following storm events, creating ephemeral waterbodies ('dry' ponds; Collins et al., 2010; Bettez and Groffman, 2012), or designed to maintain a permanent pool of water ('wet' ponds; see example pond pictures in the graphical abstract). Building a wet pond, compared to a dry pond, could reduce habitat nutrient availability for plants (wet ponds have phytoplankton for nutrient uptake), increase habitat stability (i.e., wet permanent vs. dry temporary waterbodies), and increase habitat heterogeneity (wet ponds have a mixture of terrestrial and aquatic habitat zone types; Holtmann et al., 2019), subsequently affecting invasibility. Post-construction pond management intensity also varies among and within cities depending upon socioeconomic factors and ownership; city, county, or state governments focus on removing vegetation, debris and sediment to maintain hydrologic function (Lawrence et al., 1996), while businesses or homeowners prioritize aesthetics (Monaghan et al., 2016). Ponds in less affluent cities or city sections, or with owners that desire a more natural ecosystem, may not be managed at all. Heterogeneity in pond management intensity creates a gradient from 'unmanaged' to 'actively managed' ecosystems (see pond pictures in the graphical abstract), which can affect overall plant diversity (Bean and Dukes, 2016) and therefore plant invasion.

In addition to our poor understanding of whether widespread urban pond construction practices may be facilitating biological invasions, and how ecosystem context affects these invasions, we also do not know how large a problem this knowledge gap presents because the number of stormwater ponds is currently unknown. Estimates of pond quantity are rare and generally localized (Bartout et al., 2015), which is an issue especially germane to manufactured urban ponds which are poorly studied and typically overlooked as an ecological component of the aquatic landscape. One survey of US EPA officials suggests that, in the US, stormwater ponds are the most commonly utilized stormwater control feature (Collins et al., 2010). Similarly, Tixier et al. (2011) write that tens of thousands of stormwater ponds have been built throughout North America, Europe and Australia, but it is unclear what data is the source of this estimate. Surveys have also identified thousands of ponds built across the southeastern US (Siewicki et al., 2007; Beckingham et al., 2019), with rates of pond construction in this region generally matching the pace of urban land expansion (Smith et al., 2018). This small handful of studies hints at the magnitude and thus ecological importance of stormwater pond proliferation. It is possible that, as a known side effect of urban expansion, the need to manage runoff from impervious surfaces has concomitantly resulted in stormwater ponds becoming a common and widespread feature in modern urban watersheds. However, more solid evidence at a broader spatial scale is required to support that assertion.

Small, artificial urban waterbodies are an integral component of ongoing development, a purveyor of urban ecological services, and a principal point of interaction between cities and surrounding natural ecosystems. These factors lend urgency to understanding their spatial coverage and ecological impacts. Our study sought to address knowledge gaps of how many stormwater ponds have been built as a result of urbanization, the potential negative ecological role of these ponds as habitat for invasive plants, and how pond context affects invasion by answering three principal questions: (1) what is the spatial distribution and area covered by stormwater ponds in a rapidly urbanizing region; (2) what is the degree and compositional variability of pond plant invasion; and (3) how do three key pond characteristics — type, management, and soil and water chemistry — affect plant invasion? We predict that stormwater ponds, which are heavily relied upon in urban and urbanizing regions as a BMP, are likely to be broadly distributed in our rapidly urbanizing study region. We also predict, based on known stormwater pond environmental characteristics (i.e., dynamic hydrology, nutrient-rich and urban location), that these ponds will harbor invasive plants. Furthermore, we predict that dry ponds may have greater invasive cover than wet ponds due to greater nutrient availability and more dynamic hydrology, while wet ponds may exhibit greater invasive species richness due to their combination of terrestrial and aquatic habitats, i.e., greater habitat diversity (Melbourne et al., 2007). Additionally, we predict that actively managing stormwater ponds will reduce invasion by controlling the establishment of unwanted plants.

2. Materials and methods

2.1. Study system

We addressed our objectives within the context of Florida, US. This state is an ideal study region because it is rapidly urbanizing (Terando et al., 2014), stormwater control features are common due to Florida's shallow water table and high rainfall, and Florida hosts a diverse array of invasive plants.

2.2. Quantity, coverage, and spatial distribution of stormwater ponds

To quantify stormwater pond distribution and coverage across Florida, we developed a map of constructed waterbodies ("Reservoirs" in the 1998–2012 24 k Florida National Hydrography Dataset, NHD) within 50 m of urban and built up areas and roads of Florida (based on 2012–2017 state-level urban land use codes and 2018 US TIGER/Line data for primary and secondary roads). We then excluded from this map several large constructed waterbodies (>1.5 km^2) that we knew were not stormwater ponds, and constructed waterbodies intersecting areas for agriculture, rural housing, military use, golf courses, waste treatment, and resource extraction or processing. This removal process greatly increased the likelihood that any remaining constructed waterbodies were those built for urban stormwater management (see Appendix A.1 for the pond map shapefile and further details on stormwater pond identification). Pond quantity was calculated as the total number of individual waterbody polygons in the final map and coverage was calculated as the total spatial area of these polygons. We assessed resulting map accuracy using 737 possible stormwater ponds in Gainesville, FL, US, a subset of the total identified in our Florida stormwater pond map. Using a 2018 map of the Gainesville stormwater network (City of Gainesville; personal communication), satellite imagery, and in-person visits of around 70 ponds, we estimated pond map accuracy at approximately 99% for this city (Fig. A.1).

2.3. Invasive plant survey

To assess invasive plant composition and variability across stormwater ponds (Objective 2) and determine key influences on pond invasion (Objective 3), we conducted visual surveys of stormwater ponds from 13-Jul-2018 to 31-Aug-2018 across Gainesville, FL, US. The survey was designed to compare 15 dry to 15 wet ponds (the pond 'type' categories; N = 30) that were managed at either low, medium or high levels ($n = 5$ within each management level; management categorization is detailed further below), creating a 2x3 factorial design of pond type $\times$ management intensity. Stormwater ponds in this region are relevant for addressing our study objectives because both dry and wet ponds are utilized, with the former tending to be built on well-drained soils and the latter on poorly-drained soils. High within-city variability in pond management practices has also created a gradient of unmanaged to actively managed ecosystems. Importantly, these differences in how stormwater ponds are built and managed can be captured within one geographic area, which better controls for ecosystem variability in climate, development history and background of plant introductions. The majority of the stormwater ponds in our study region tend to be built via shallow excavations (average depth of sampled ponds = 1.7 m; Table A.1) and designed with vegetated perimeters with direct contact between collected runoff and soil substrates. Stormwater ponds can be built with concrete walls along their margins and synthetic liners to reduce infiltration; however, such ponds are rare in our study region and were not included in our survey. Additional details on the location, morphology and land use context of surveyed ponds can be found in Table A.1.

Survey ponds were selected within Gainesville proper and its urban cluster, which was divided into 127 'neighborhoods' delineated based on shared residential, commercial and industrial complexes. Neighborhoods were randomized, without replacement, and only one pond was selected from each neighborhood (to minimize spatial autocorrelation) in succession until all ponds that satisfied the survey design had been found (Fig. A.2). Additional restrictions were: (1) ponds had to be less than 0.01 km^2 in size (~90% of potential ponds) to preclude the influence of rare, large ponds; and (3) within each pond type $\times$ management category, we ensured that years of construction spanned evenly from 1980 to 2010 (Table A.1), thus controlling for variance in pond age and allowing sufficient time for invasive plant establishment.

Pond management was characterized according to management frequency of 'outer' and 'inner' pond sections. Outer pond sections include areas where the upper pond bank flattens, i.e., the upland edge, down to the lower end of the bank slope. This pond section is never or rarely inundated with water, which was assessed based on pond design, overflow structures and the absence of emergent aquatic plants. Pond inner sections were those areas designed to be temporarily or permanently inundated with water, which were delineated using pond bases, permanent standing water and areas bounded by emergent aquatic vegetation. Active pond vegetation management in outer sections is commonly accomplished via mowing, removal of plant debris and litter, and applications of pesticides and herbicides. Inner pond sections are generally managed via removal of unwanted aquatic plants, applications of algaecides, and usage of fountains or bubblers for aeration. Outer and inner pond sections that received no active management were scored as 0, sections managed approximately once per year as 1, sections consistently managed monthly, seasonally, or as needed as 2, and sections both consistently managed and purposefully planted as 3. Ponds with a total score summed across inner and outer sections of 0–1 were categorized as 'low' management, 2–3 as 'medium' and 4–5 as 'high'. Ponds scored as 6 were rare and therefore excluded.

2.4. Sampling design

Vegetation surveys were conducted in pond outer and inner sections. All terrestrial, semi-aquatic and aquatic invasive plants within the pond were documented, up to 2 m outside the upland edge. Invasive plant species total aerial cover was recorded separately for outer and inner pond sections at 10% intervals from 0–100%, with rare plants recorded as <1% cover (treated as 0.5% in all analyses). We considered a species invasive if it was classified as such by the 2017 Florida Exotic Pest Plant Council (www.fleppc.org; both category I and II) or if it was a non-native recorded in Alachua County, FL and considered potentially invasive in the Southern US by the US Department of Agriculture. Invasive plants were identified to species using a list of unique characteristics for the 81 plant invaders already vouchered in Alachua County, FL. Any plants that could not be identified in the field were collected and later identified by the Plant Identification and Information Service at the University of Florida Herbarium.

As stormwater pond environmental characteristics (e.g., nutrients) can drive plant invasions, we measured pond chemistry by collecting 15 cm deep soil samples from all pond outer sections, 5 cm deep sediment samples from all pond inner sections, and water grab samples from wet pond inner sections. All samples were measured for ammonium-nitrogen (Soil: mg kg^{-1}; Water: mg L^{-1}), nitrate-nitrogen (Soil: mg kg^{-1}; Water: mg L^{-1}), organic nitrogen (total Kjeldahl nitrogen minus ammonium-nitrogen; Soil: mg kg^{-1}; Water: mg L^{-1}) and pH (analyzed as mol L^{-1} of hydrogen ions). Soil and sediment samples were also measured for Mehlich-III extractable phosphorus (mg kg^{-1}) and organic matter (%), while ortho-phosphate (μg L^{-1}) and total phosphorus (μg L^{-1}) were also measured in water samples. Samples were processed at the UF|IFAS Analytical Services Laboratories following standard EPA methods, excepting organic matter quantified via loss-on-ignition in the Urban Ecosystem Ecology Lab at UF.

2.5. Statistical analyses

Using species presence/absence data, we calculated the Simpson's dissimilarity index of the invasive plant communities within pond type and management categories to quantitatively compare spatial turnover in plant species composition (i.e., a major component of beta diversity; Baselga, 2010). This dissimilarity index ranges from 0 to 1, with 1 indicating maximum spatial community turnover with no shared species among compared communities, allowing us to assess the degree to which ponds within the same type and management categories harbored a similar invasive species community. We also assessed the role of pond type and management intensity as drivers of invader species richness and total cover by modeling these continuous response variables against categorical predictor variables for type (dry or wet) and management (low, medium or high). Full models also contained pond age as a continuous predictor and all possible two-way interactions among predictor variables. Pond outer and inner richness and cover were each modeled separately using Poisson distributions for richness (log link; ϕ in the results indicates dispersion) and Beta distributions for cover (logit link). Full models were reduced by removing non-significant ($P > 0.05$) interactions and then individual fixed effects based on Log-likelihood Ratio Tests (LRTs) as described by Zuur et al. (2009). Model reduction concluded when only significant predictors or the null model remained (see Table A.2 for final models).

We used Redundancy Analysis (RDA) to assess the degree to which soil, sediment and water chemistry affected invader establishment and cover (Objective 3). Two RDAs were conducted, one that modeled invasive richness and cover in all dry and wet pond outer and inner sections in response to all soil and sediment chemistry variables, and one that modeled wet pond invasive richness and cover in relation to water chemistry. To determine whether constraining RDA chemistry predictor variables explained significant variation in invasive plant cover and richness, we sequentially removed correlated predictors with the highest variance inflation factors (until all were <10), then removed predictors whose exclusion improved the adjusted R^2 (R^2_{adj}) of the models. Overall significance of remaining constraining chemistry predictors was determined using global permutation tests (GPT; Legendre and Legendre, 2012). For significant RDAs, we then tested whether pond type and/or management categories were located in significantly different positions in the RDA (i.e., whether chemistry-related patterns in invasion corresponded to differences in pond type or management) using non-parametric permutational multivariate analyses of variance (PERMANOVA; Anderson, 2001). These analyses used the Euclidean distance matrices of site positions in the RDAs as the response variables. Categorical predictor variables were either pond type, management and their interaction (soil and sediment PERMANOVA) or just management (water chemistry PERMANOVA).

All statistical analyses were performed in R 3.5.0 (R Core Team, 2018) using the 'betareg' (v3.1-1; Cribari-Neto and Zeileis, 2010) and 'vegan' (v2.5-2; Oksanen et al., 2018) packages. All multivariate significance tests were performed using Euclidean distance with 10,000 permutations.

3. Results

3.1. Quantity, coverage, and spatial distribution of stormwater ponds

We identified 76,059 stormwater ponds (Fig. 1a) covering a total area of 627 km^2. This coverage represents 2.7% of the total urban land cover of Florida (23,870 km^2 total) and is similar to other major urban land use types such as industrial, recreational, and institutional land (Fig. 1b). The greatest density of ponds occurred in and around metropolitan areas and highways. Large gaps in coverage occurred in rural or undeveloped areas such as national parks.

3.2. Degree of pond invasion and compositional dissimilarity of invasive plant communities

Ninety-six percent of sampled ponds (29/30) contained one or more of 28 different invasive plant species (Fig. 2a; Table A.3). Most species occurred in a third or less of surveyed ponds, with only two species, *Triadica sebifera* (Chinese tallow) and *Alternanthera philoxeroides* (Alligator weed), occurring in approximately 50% of ponds. In fact, high Simpson's dissimilarity indices in dry and wet ponds (0.83 and 0.77 respectively), and low, medium and high management ponds (0.76, 0.78 and 0.76), indicated that even ponds from the same type (dry or wet) and management cat-

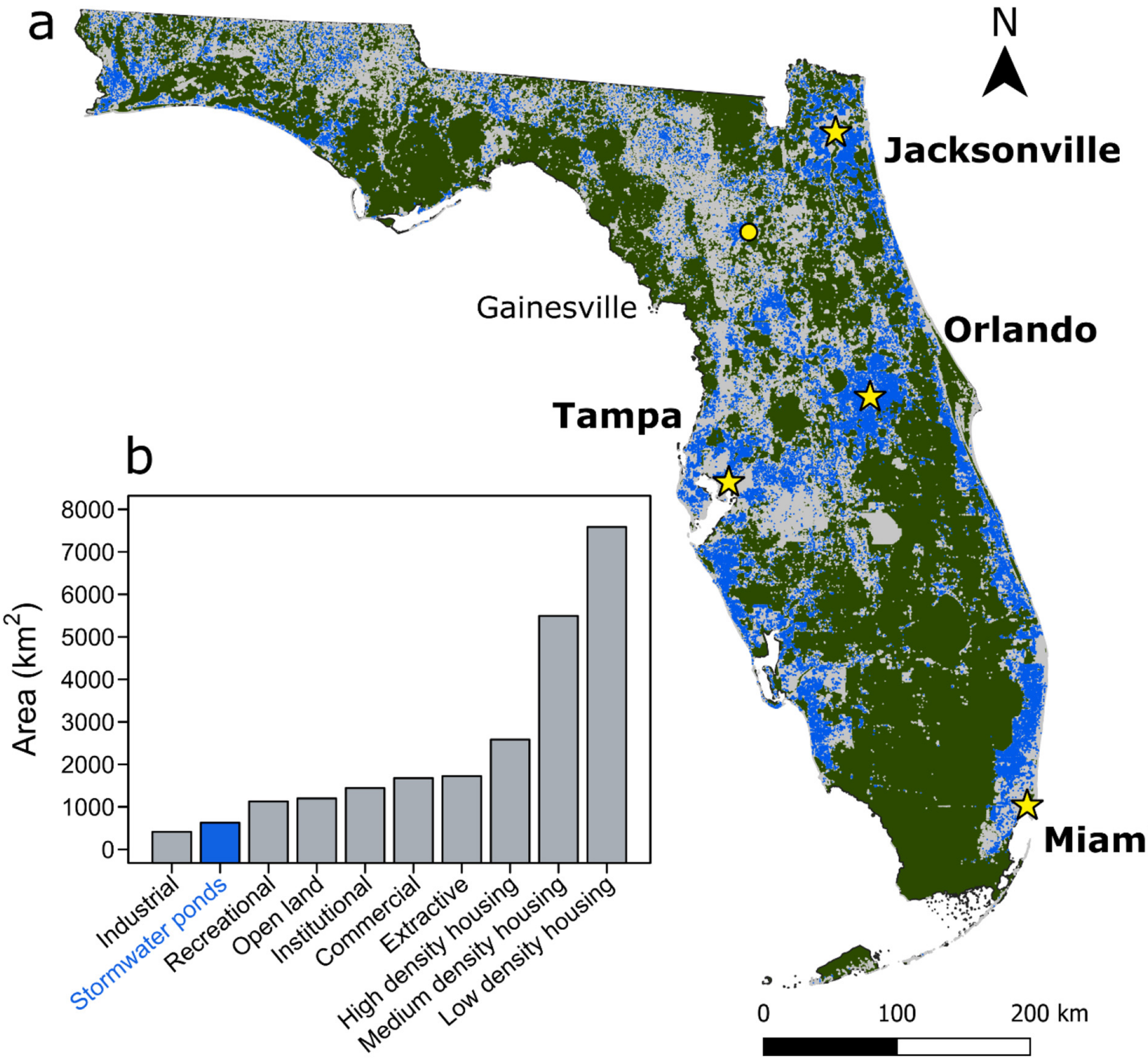

Fig. 1. Coverage of urban stormwater ponds (blue) and all urban/built-up areas and roads (grey) in Florida, USA (green). There are (a) over 76,000 stormwater ponds in the state and (b) stormwater ponds, compared to other urban and built-up land cover types, have become a common feature of Floridian urban landscapes. This map also illustrates that stormwater ponds tend to be concentrated around major cities (yellow stars; Gainesville indicated by a yellow circle) and transportation routes, providing a potential habitat network for the spread of invasive species.

egory (low, medium or high) exhibited little commonality in invasive plant composition. Invasive plant richness across pond types and outer and inner sections ranged from 0 to 10 species (Fig. 2b), while cover ranged from 0 to 82% (Fig. 2c).

3.3. Invasive plant species richness

In pond outer sections, dry ponds had overall higher invasive species richness compared to wet ponds (Dry: 3.7 ± 0.9 species; Wet: 2.3 ± 0.4; mean ± SE). Invasive richness tended to decline as management increased, however the magnitude of this decline was greater in dry compared to wet ponds (evidenced by a significant Type*Management interaction; LRT, n = 30, L = 13.54, df = 2, P = 0.001; ϕ = 1.3; Table A.2). Invasive species richness in dry pond outer sections decreased by 93% as management intensity increased from low to high (5.8 ± 1.3 species down to 0.4 ± 0.4), whereas wet pond richness only decreased by 38% (3.2 ± 0.6 down to 2.0 ± 0.3; Fig. 3a vs. b).

In pond inner sections, there was little difference in invasive richness between dry and wet ponds (Dry: 1.8 ± 0.4 species; Wet: 1.7 ± 0.3), with evidence only for a decline in richness as management increased (marginally non-significant Management effect; LRT, n = 30, L = 5.72, df = 2, P = 0.057; ϕ = 0.7; Table A.2). Invasive species richness in combined dry and wet pond inner sections decreased by 56% as management intensity increased from low to high (2.3 ± 0.4 species down to 1.0 ± 0.2; Fig. 3c vs. d).

3.4. Invasive plant total cover

In pond outer sections, dry ponds had overall higher invasive cover compared to wet ponds (Dry: 13 ± 3%; Wet: 4 ± 2%). Invasive cover tended to decline as management increased, however the magnitude of this decline was again greater in dry compared to wet ponds (evidenced by a significant Type*Management interaction; LRT, n = 30, L = 7.09, df = 2, P = 0.029; Table A.2). Invasive cover in dry pond outer sections declined from 20 ± 4% at low management down to 1 ± 1% at high, whereas wet pond cover declined from 7 ± 5% down to 1 ± 1% (Fig. 3e vs. f). Additionally, there was evidence for an increase in outer invasive cover in older wet ponds, but not dry ponds (significant Type*Age interaction; LRT, n = 30,

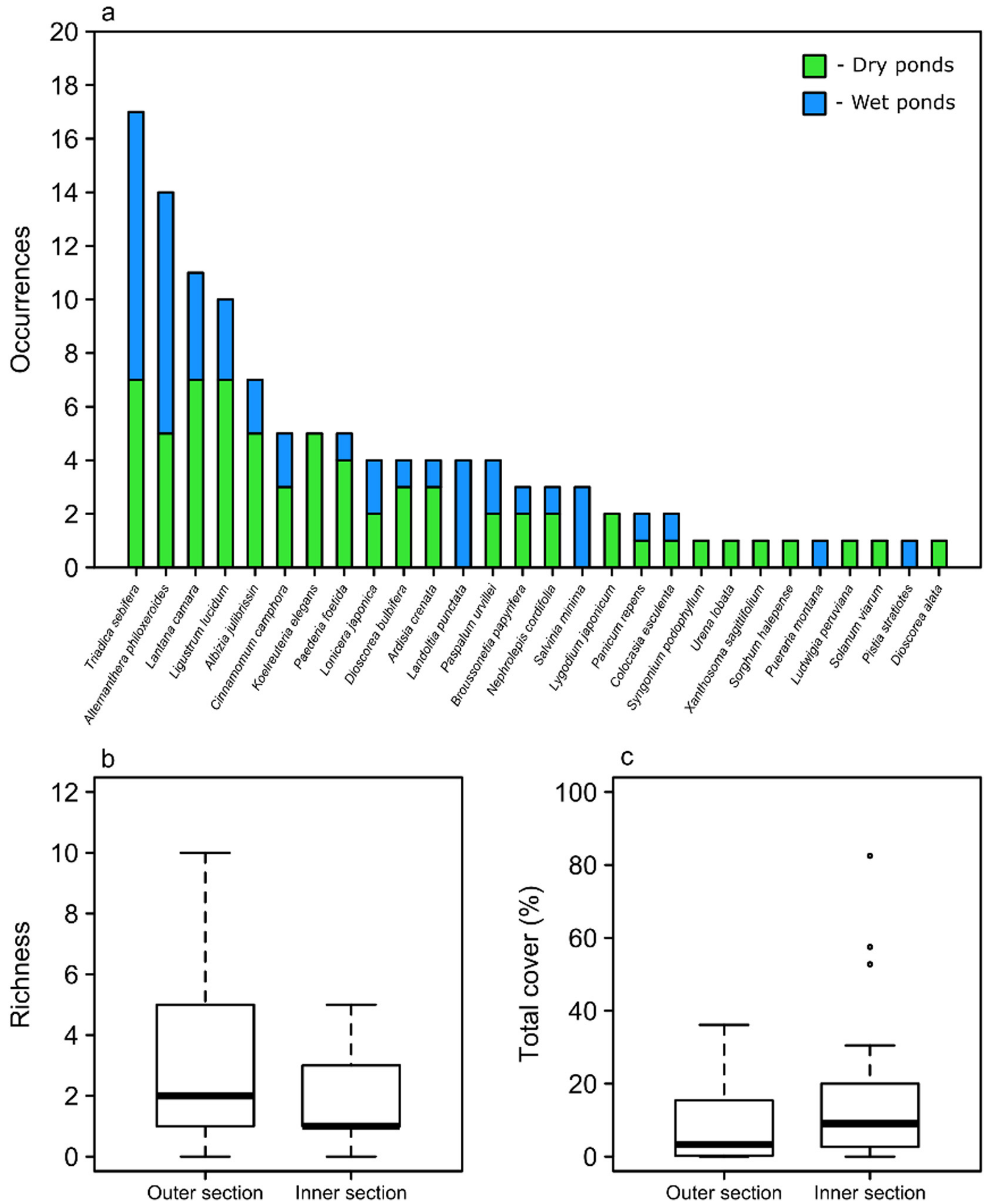

Fig. 2. (a) The number of ponds out of 30 (dry and wet) in which each of the detected 28 invasive plant species occurred, and the overall range in invasive (b) species richness and (c) total cover in the outer and inner sections of all ponds (N = 30). Note that (a) most detected invasive plant species occurred in a third or less of ponds, and that there was a wide range in invasive plant species (b) richness and (c) cover.

L = 4.40, *df* = 1, *P* = 0.036; Table A.2). Dry pond cover remained constant across decades around 12%, while wet pond cover increased over time from 0% in ponds built around 2007 to 11% around 1980 (Fig. A.3).

In pond inner sections, there was no strong difference in invasive cover between dry and wet ponds (Dry: 11 ± 5%; Wet: 19 ± 6%). Increasing management intensity tended to reduce invasive cover in dry ponds, but had variable effects in wet ponds (evidenced by a significant Type*Management interaction; LRT, *n* = 30, *L* = 7.17, *df* = 2; *P* = 0.028; Table A.2). Dry pond invasive cover declined from 23 ± 8% at low management down to 6.0 ± 4% at high (Fig. 3g). Conversely, wet pond cover increased from low (18 ± 10%) to medium management (34 ± 12%), then declined at high (down to 5 ± 2%; Fig. 3h).

3.5. Relationship between pond chemistry and invasion

Across all ponds, invasive plant cover and richness tended to increase with increasing soil nutrients (evidenced by a significant GPT; *n* = 30, R^2_{adj} = 0.21, $F_{4,29}$ = 2.95, *P* = 0.011; Fig. 4a), a pattern driven by inner section nitrogen and phosphorus, with no detected effects of water chemistry on plant invasion (GPT; *n* = 15, R^2_{adj} = 0.1, $F_{5,14}$ = 1.3, *P* = 0.28; Fig. A.4). There were no apparent differences between dry vs. wet ponds in the relationship between soil and sediment chemistry and invasive richness and cover (Fig. 4a). However, increasing management intensity in dry ponds matched associated declines in soil and sediment organic matter and nutrient concentrations that related to invasive richness and cover (moving from right to left primarily along RDA axis 1; Fig. 4b), but manage-

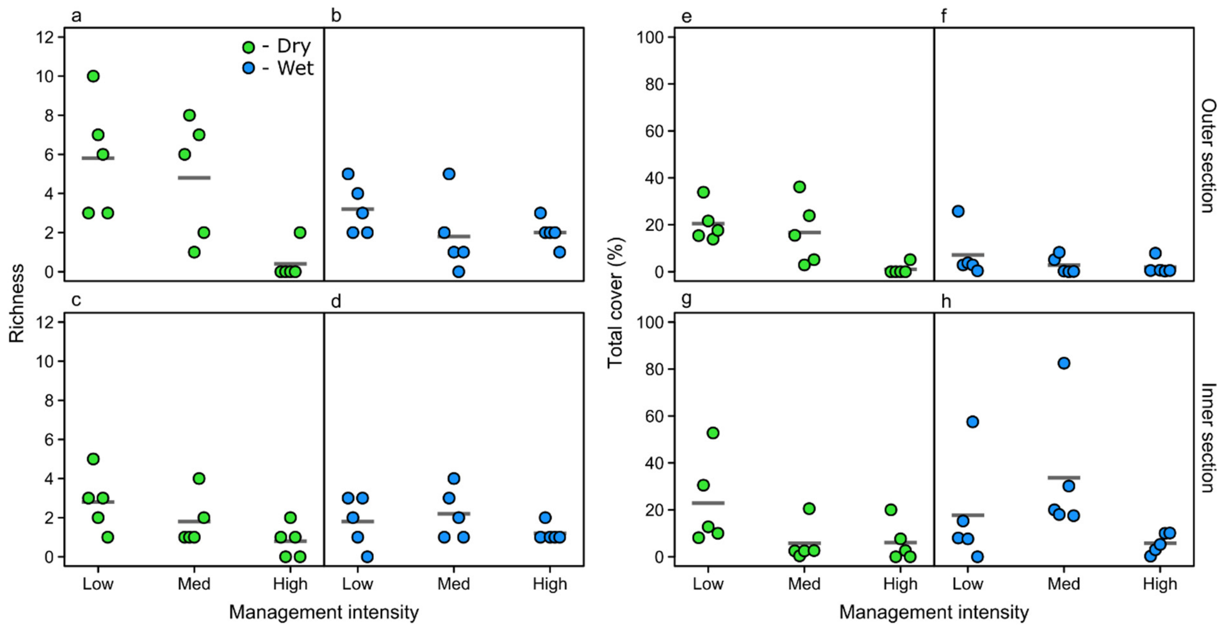

Fig. 3. Invasive plant (a–d) species richness and (e–h) total cover in pond outer and inner sections (upper and lower row, respectively) of dry and wet ponds (blue and green, respectively) managed at low, medium and high intensities (x-axis). Pond type and management interacted to determine the extent of plant invasion. Dry, low management ponds tended to exhibit the highest (a, c) invasive richness and (e, g) cover in both outer and inner pond sections. More intense management also reduced invader richness and cover in dry ponds, but had a reduced effect on invader richness and cover in (b, f) wet pond outer sections. Conversely, management tended to increase (d, h) wet pond inner section invader richness and cover, specifically at medium intensities. Thirty stormwater ponds (N = 30) were sampled to produce the richness and cover data points for the outer and inner section plots of dry and wet ponds. Means for each pond type and management category grouping are also represented by grey lines within each point cluster.

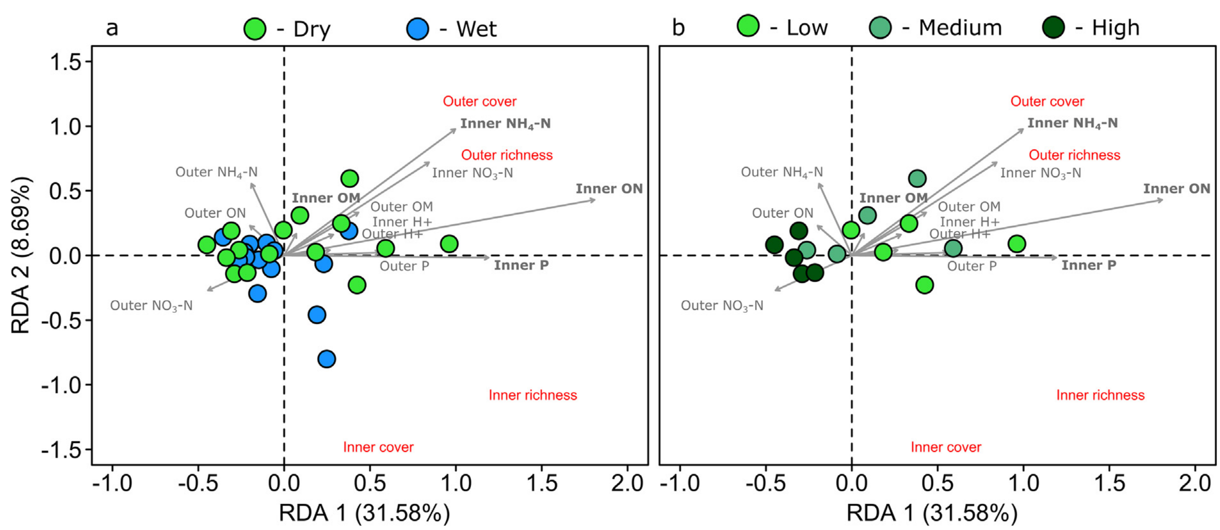

Fig. 4. Redundancy analysis (RDA) of invasive plant species richness and total cover in pond outer and inner sections in relation to pond soil (outer) and sediment (inner) chemistry (N = 30). Color overlays are plotted for (a) pond type and (b) dry pond management intensity to illustrate the principal results. There were no strong differences between dry vs. wet ponds in how pond chemistry related to invasive cover or richness, evidenced by dry and wet ponds clustering together (a). However, there were several highly invaded dry ponds which also had higher concentrations of soil and sediment nutrients. These highly invaded dry ponds with higher nutrients were primarily low and medium management ponds (b). Letters 'H+', 'NH_4-N', 'NO_3-N', 'OM', 'ON', and 'P' refer to hydrogen ion, ammonium-nitrogen, nitrate-nitrogen, organic matter, organic nitrogen, and phosphorus concentrations respectively. Chemistry predictors retained in the final soil and sediment RDA model are in bold.

ment intensity had no apparent association to wet pond soil and sediment chemistry in relation to invasion (evidenced by a significant Type*Management interaction; PERMANOVA, n = 30, R^2 = 0.12, $F_{2,29}$ = 2.25, P = 0.047; Fig. A.5).

4. Discussion

The high quantity of stormwater ponds (76,000) that we found in a rapidly urbanizing region of the US (Florida) was surprising given that 'tens of thousands' was one suggested number of stormwater ponds across three continents (Tixier et al., 2011), whereas we found pond quantity to be closer to an order of magnitude higher than this estimate in just a single US state. Stormwater ponds may have become so common in our study region because they are well-understood due to their long history of use, and they have a more standard design, cost less to build, and can be easier to maintain compared to other runoff management methods (Weiss et al., 2011). While we cannot extrapolate our pond quantity estimate to scales broader than Florida, our results provide one of the first glimpses into the sheer regional scale of pond quantity and coverage that has resulted from widespread stormwater pond construction, informing the possible ecological role played by these ecosystems in facilitating plant invasions. Additionally, the quantity of ponds we identified just in Florida suggest there are at least hundreds of thousands of total stormwater ponds concentrated in urban and urbanizing areas across the globe, although broader-scale research is required to confirm this inference. Such extensive pond usage could create an artificial 'pondscape' of habitats that may act as steppingstones for any species they harbor to spread across urban landscapes (Hassall, 2014; Hill et al., 2017), which could be further aided by pond connections to downstream municipal stormwater conveyance networks that ultimately flow into natural waterbodies.

The unexpectedly high quantity of stormwater ponds we identified in Florida underlines the need to improve data quality and better quantify pond coverage at broader spatial scales. Our stormwater pond map undoubtedly provides a conservative estimate. Only waterbodies built as of 2012 are included and we excluded thousands of waterbodies similar to stormwater ponds (i.e., small area with straight margins and no vegetation) that either overlapped excluded areas, such as golf courses, or were classified as natural "Lakes or Ponds" in the NHD, many of which could be constructed stormwater ponds. Data reliability on stormwater pond quantity also varies widely among US states and likely other countries. As an example, there are potentially thousands of stormwater retention basins in Phoenix, AZ (Larson and Grimm, 2012), but the Arizona NHD only lists about 460 reservoirs in the entirety of this state's urban regions. There are other available US datasets that include urban ponds, such as the National Wetlands Inventory (NWI). However, more than 25% of the stormwater ponds identified in our map were not in the NWI. Data gaps in the NHD or NWI are likely due to difficulties in identifying the finer-scale changes in topography of small waterbodies using current remote sensing techniques, although LIDAR may prove more effective (Larson and Grimm, 2012).

Almost all surveyed ponds contained at least one invasive plant species, which matched our initial predictions, but overall species richness was surprisingly high at 28 different invaders identified across only 30 ponds. Species turnover was also generally high within pond type and management categories, and many ponds harbored multiple invaders or exhibited greater than 10% invasive cover (Fig. 2). In terms of total invasive plant species diversity, these ponds are similar to urban gardens into which invasive plants are often purposefully introduced (e.g., 17–25 total invasive plant species in urban gardens surveyed by: Marco et al., 2008, 2010; Bigirimana et al., 2012; Padullés Cubino et al., 2015). Stormwater ponds may also tend to harbor more invasive plants than other designed ecosystems such as green roofs (Bates et al., 2013; Madre et al., 2014), lawns (Bertoncini et al., 2012) or recreational parks (Barrico et al., 2012; Hüse et al., 2016; Talal and Santelmann, 2019), which studies have so far determined tend to harbor only a handful of invasive plant species. Additionally, we found just a few instances of purposeful invasive plantings in the surveyed ponds, which is interesting because it indicates most invaders were colonists. Given the similar invasion levels between stormwater ponds and urban gardens, and that most invaders likely colonized the ponds, these factors suggest intentional plantings elsewhere in the surrounding urban landscape or watershed (e.g., gardens, decorative ponds or aquariums) may be the source of many pond invaders. Further research is needed to determine whether the high diversity of stormwater pond invaders we found applies at broader scales or to different study regions. Florida harbors a wide variety of invasive plants, which could suggest our high diversity results are only regionally applicable. Conversely, it is possible our survey provides a *conservative* estimate of invader diversity. For example, the garden surveys referenced above sampled around 100 to over 1000 ecosystems and found similar invasive plant diversity to what we detected across only 30 urban stormwater ponds. A larger survey may therefore have determined that stormwater ponds can harbor an even greater diversity of invasive plant species.

To compare the invasion of surveyed stormwater ponds to natural ecosystems, we used the University of Georgia Early Detection and Distribution Mapping System (EDDMaps, www.eddmaps.org) to determine which invasive pond plants can also occur in natural wetlands within the urbanized area of Gainesville. Of the 28 total invasive plant species identified in surveyed stormwater ponds, 26 have also been recorded in city wetlands. This shared invasive species pool among urban wetlands and stormwater ponds could present a conservation problem. Despite the relative simplicity of a manufactured stormwater pond, our invasive plant survey and EDDMaps results show that stormwater ponds are functioning as habitat for a wide variety of invasive wetland plants. Stormwater ponds and their ongoing proliferation may therefore be augmenting habitat availability for invaders that can harm wetland communities. However, our study cannot disentangle whether invasive plants first arrived and established in stormwater ponds then dispersed into natural urban wetlands, or whether stormwater ponds just added more invasible habitat to urban landscapes (or both).

Greater plant invasion in dry relative to wet ponds, both at lower management intensities and over time, was potentially linked to higher nutrient concentrations or greater habitat variability. Nutrient removal efficiency varies across stormwater ponds (Reisinger et al., 2016) and pond types. Dry ponds can be less effective than wet ponds at removing nutrients (Collins et al., 2010; Koch et al., 2014) because they do not hold water for extended periods, limiting sedimentation of soluble pollutants (Collins et al., 2010), and dry ponds have fewer avenues for nutrient assimilation into non-plant community components (e.g., little to no phytoplankton). This potential for lower, non-plant nutrient removal in dry ponds could theoretically provide more resources for invasive plant establishment, which might be absent at high management levels because potential nutrient sources, such as debris, leaves, unwanted vegetation and sediment blockages, are cleaned out (suggested by a decrease in dry pond nutrients at high management; Fig. 4b). Highly managed dry ponds could thus exhibit reduced invasion due to both the management of vegetation and/or removal of nutrients. Alternatively, higher dry pond invasion could be driven by greater habitat variability. Dry pond water levels fluctuate more than those of wet ponds, producing more dynamic environmental conditions which can increase establishment opportunities for invasive plants (Davis et al., 2000). Additionally, invasive species tend to have broad ecological tolerances (Richards et al., 2006) that may facilitate dominance in the more variable habitat of dry ponds.

The inner sections of wet ponds exhibited greater invasion at medium levels of management possibly because these ponds tend to combine a typically unmanaged inner section with a less accessible and disturbed outer section. Medium managed ponds are generally maintained for function rather than aesthetics. Properly managing vegetation in wet pond inner sections is also more difficult and expensive: heavy machinery (e.g., mowers) cannot access wet pond inner sections, it is difficult and dangerous to approach the water's edge, and aquatic systems require additional management skills and training. When these restrictions are applied to wet ponds for which aesthetics are unimportant, the typical result is a pond with an unmanaged inner section and unmanaged portions of the outer section close to the water, providing refuges for invasive plant establishment and persistence. Additionally, disturbance from what management does occur in the outer section, and maintenance machinery that can transport propagules among ponds, could further facilitate plant invasion. Medium managed wet ponds may therefore be experiencing some combination of less-effective management, along with disturbance and increased propagule pressure in the outer section that is promoting plant invasion.

4.1. Practical implications

Stormwater ponds present a unique opportunity to improve urban green space as they are often the only type of aquatic habitat city residents can access and interact with (Wendel et al., 2011; Warner et al., 2019). However, managing stormwater pond invasion could be challenging for urban areas that combine high invasive plant diversity, as occurred in our survey, with a high diversity of stakeholders and landowners with differing goals for pond management. As an example, our 30-pond survey in a single city required the cooperation of 22 different agencies. Maintaining pond hydrologic function via regular management of overall pond vegetation through mowing, debris clearance and sediment removal are established and straightforward pond management methodologies, shared across agencies, which we also found reduced plant invasion. Unfortunately, intensive plant selection and pond maintenance, which can include the application of pesticides and herbicides, is not always affordable and can come with added ecological costs to non-target organisms. Management methods that denude pond vegetation (e.g., a closely mowed outer section) can also compromise pond functions that rely upon terrestrial and aquatic plants, such as water quality and carbon sequestration (Moore and Hunt, 2012). 'Hands-off' management is an alternate solution. We found some unmanaged ponds over a decade old with low invader presence (e.g., 1–2 species at less than 10% cover) suggesting that minimal management can allow for self-organization of stormwater pond plant communities that resist invasion. Creating stormwater ponds that fulfill their intended hydrologic functions with less managed, non-invasive vegetation would be a valuable addition to the growing suite of urban green spaces. It is, however, unclear what mechanisms drive variable invasion resistance among unmanaged pond communities (e.g., traits of resident native or non-native plants, competitive interactions, niche availability).

5. Conclusions

Stormwater ponds are a commonly recommended urban hydrologic control measure that could facilitate the establishment and spread of invasive species. We must therefore improve the understanding and management of these designed ecosystems to minimize their ecological impacts. Our research shows the magnitude at which urbanization can drive the proliferation of stormwater ponds, providing thousands of new colonizable habitats. Many of these ponds could harbor abundant or diverse communities of invasive plants. We also found that invasion severity was influenced by pond type and management intensity, and varies relative to soil and water chemistry, with invasion highest in the unmanaged dry ponds and medium managed wet ponds of our study region. We have also highlighted fruitful avenues for future research and applied invader control, such as the need for broader-scale pond coverage analyses and surveys, investigations of non-linear relationships between invasion and pond characteristics, the effectiveness of traditional pond management practices, and possible effectiveness of hands-off management.

Additionally, we examined the negative ecological role of stormwater ecosystems through the perspective of biological invasions, however this question is a microcosm of a broader question of ecological services and disservices in designed ecosystems. Urbanization is proliferating multiple types of manufactured green infrastructure, such as gardens, lawns, parks and other urban ponds. These systems, and the ways in which they are distributed, constructed and managed can contribute crucial, beneficial ecological functions to urban landscapes, but can also create associated negative ecological impacts. Our research supports the contention that urban development must include a conservation focus, similar to those principles applied when building ecosystems in restoration or reconciliation ecology, to optimize the positive and minimize the negative contributions of increasingly common designed ecosystems.

Author contributions

JSS led the data collection. AJR contributed to the chemical analyses, EB to the stormwater pond map, and CRA to the plant survey. BVI, AJR, EB and CRA conceived of and designed the study. All authors contributed to analyses and writing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to the City of Gainesville and Alachua County Public Works, the School Board of Alachua County, Gainesville citizens, Michelle Atkinson, and Marc Frank (UF|IFAS Extension Herbarium) for their assistance. This work was supported by Florida Agricultural Experiment Station, the UF|IFAS Program for Resource Efficient Communities, and USDA McIntire-Stennis Capacity Grant (1012120).

Data statement

Data is publicly available from the Institutional Repository at the University of Florida at https://ufdc.ufl.edu/IR00011021/00001/citation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.135133.

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