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High similarity and management-driven differences in the traits of a diverse pool of invasive stormwater pond plants

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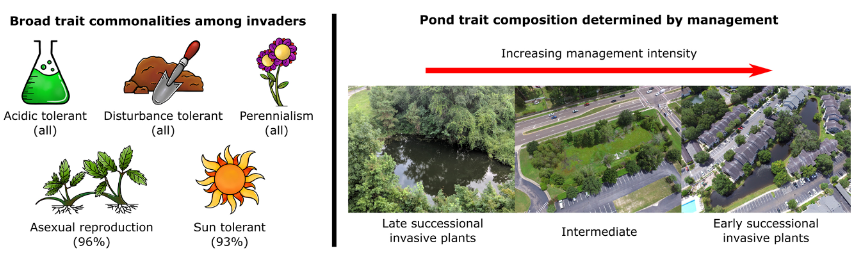
G R A P H I C A L A B S T R A C T



1. Introduction

Urbanization is a principal cause of declines in natural habitat and native species (McKinney, 2002), but also drives the creation of new ecosystems such as gardens, lawns and urban ponds ('designed ecosystems'). These manufactured habitats can provide valuable ecosystem services (e.g., food and aesthetics; Haase et al., 2014) and can harbor diverse biological communities which improve urban ecological function (Goddard, Dougill, & Benton, 2010; Hassall, 2014). Given designed ecosystems are a major component of growing urban land cover (Loram, Tratalos, Warren, & Gaston, 2007; Robbins & Birkenholtz, 2003), understanding which species colonize these ecosystems is therefore increasingly important to the ecology and management of cities and urban-associated natural areas.

The plant communities within designed ecosystems are of particular importance. Plants in urban ecosystems are the focal organism for purposeful control by people (Faeth, Bang, & Saari, 2011), and designed ecosystems provide new, colonizable habitats for plant establishment. The types of plants that either purposefully or naturally occur in designed ecosystems are also integral to important ecosystem and ecological services, such as the cultural, food and biodiversity benefits provided by home and community gardens (Lin, Philpott, & Jha, 2015). However, the positive contributions of vegetation in designed ecosystems can be compromised by the harmful impacts of invasive plants (Potgieter et al., 2017), with the terms 'invasive' or 'invader' referring to non-native species with demonstrable negative ecological or economic effects (sensu Lockwood, Hoopes, & Marchetti, 2013). Designed ecosystems are concentrated in urban centers, which are hubs for invasive plant distribution and human disturbance, two factors that frequently drive invasion (Padayachee et al., 2017; Sher & Hyatt, 1999). Designed ecosystems are also often purposefully planted with non-native ornamental species that can become invasive. Therefore, creating designed ecosystems that provide desired ecosystem services and ecological benefits requires that we understand the mechanisms determining plant establishment and unwanted invasions.

Uncovering the mechanisms structuring urban plant communities

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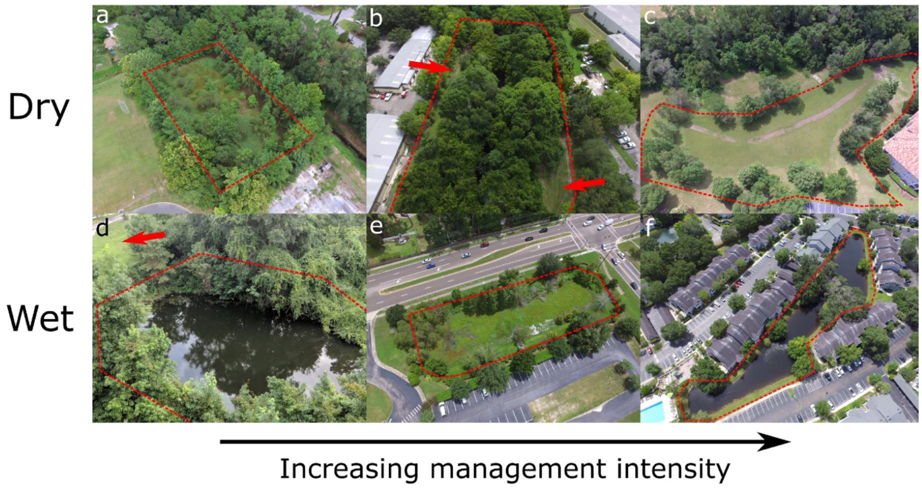

Fig. 1. Aerial photographs of example stormwater ponds in Gainesville, FL from 2018. Photos illustrate how vegetation varies with pond type (dry versus wet; a–c versus d–f respectively) and management (increasing left to right). Red outlines show approximate pond outer borders where the bankslope begins. Ponds (a) and (d) are unmanaged, although there can be managed areas outside the ponds (e.g., red arrow in d). Ponds (b) and (e) receive regular maintenance and purposeful plantings around the outer upland and bankslope (e.g., red arrows showing mowed sections in b), however their permanent or temporarily inundated inner sections are unmanaged. Ponds (c) and (f) receive regular management in both the outer and inner pond sections. Pond photographs, red outlines and arrows were all provided by James Sinclair. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

requires consideration of complex interactions between the natural (e.g., soil conditions and dispersal; Williams et al., 2009; Adler & Tanner, 2013) and anthropogenic (e.g., high impervious surface; Raciti, Hutyra, & Finzi, 2012) processes operating within urban landscapes. This complexity can result in high compositional heterogeneity, i.e. beta diversity (Swan, Pickett, Szlavecz, Warren, & Willey, 2011), even among the same type of designed ecosystems (e.g., LaPaix & Freedman, 2010; Lowenstein & Minor, 2016), making it difficult to identify general drivers of plant establishment and invasibility.

Studies of plant functional traits could provide a better avenue for identifying these broad-level mechanisms. A common set of filters, such as preferential human selection or tolerance for urban stressors (Aronson et al., 2016; Williams et al., 2009), likely determines the *types* of plants (as opposed to specific species) that occur in urban ecosystems. For example, annual life history is a common trait of plant colonizers across multiple cities (e.g., Williams, Hahs, & Vesk, 2015; Palma et al., 2017; Zeeman, McDonnell, Kendal, & Morgan, 2017), potentially due to selection for plants that can tolerate harsh and disturbed urban conditions. Focusing on traits, rather than species, can also improve research comparability across regions (Williams et al., 2015), and can reveal shared invasive plant traits and invasion pathways which can be used to improve management.

However, differences in the design and management of designed ecosystems, and a current lack of research, makes it unclear whether there are general trait-based processes that filter plant establishment. Urban plant trait research typically does not focus on designed ecosystems (but see Bertoncini, Machon, Pavoine, & Muratet, 2012; Kendal, Williams, & Williams, 2012) nor possible trait-based drivers of plant invasion in these ecosystems. Research focused on designed ecosystems is necessary because they are purposefully built and maintained by people and therefore experience unique establishment filters compared to other urban habitats, such as remnant natural systems. The construction or design practices employed are also often unique and variable within and among cities (e.g., mesic versus xeric garden designs in Phoenix, AZ, USA; Martin, 2003), as is management intensity and methods (e.g., lawn care practices; Polsky et al., 2014). Additionally, each type of designed ecosystem can have unique social drivers, such as the plant preferences of nearby residents, which influence plant trait composition (Kendal et al., 2012). Our current grasp of the ecology of designed ecosystems would therefore benefit by developing a better understanding of trait commonalities among plant colonizers, of how the design and management of individual ecosystems affects colonizer trait composition, and comparing any patterns found to those that have been identified in the broader urban flora.

To address the above knowledge gaps, we conducted a study of invasive plant traits in an increasingly common and abundant designed ecosystem: stormwater ponds. Our study had two objectives: (1) identify which traits are common to the invasive plants occurring in stormwater ponds; and (2) quantify how variation in pond type and management affects invasive plant trait composition. We selected these objectives and study system based on prior research that determined urban stormwater ponds in our study region (Gainesville, FL, USA) can be highly invaded (up to 10 species or 80% cover of invasive plants; Sinclair et al., 2020), and that the majority of these detected invasive plants colonized the ponds from elsewhere. Stormwater ponds also provide important ecosystem services that could be compromised by plant invasion. These ponds are utilized in cities across multiple continents to manage stormwater runoff from urban impervious surfaces, and the plants within affect pollutant filtering (Beckingham, Callahan, & Vulava, 2019) and aesthetics. Determining the common traits of invasive plants in stormwater ponds could therefore help to pinpoint what, if any, general mechanisms might be driving plant colonization in these important ecosystems, and would contribute to improving invader prevention and control.

Additionally, there are a variety of stormwater pond types and management regimes, providing an ideal study system to determine how ecosystem design and management practices affect colonizer trait composition (Fig. 1). 'Dry' retention stormwater ponds are typically built to drain within a few days of a rain event, creating ephemeral aquatic habitat, while 'wet' detention ponds have a consistent pool of water, creating permanent aquatic habitat (McCarthy & Lathrop, 2011). Establishment opportunities for invasive plants with different traits, such as drought versus flood tolerant species, could thus depend upon the type of pond built. Pond management practices also vary with institutional jurisdiction and socioeconomic investment. Businesses and homeowners tend to create aesthetically pleasing ponds, while state, county and city governments tend to only remove vegetation and debris that impair pond function (Bean & Dukes, 2016). Some ponds are also almost completely unmanaged, with overgrown and wild vegetation. This gradient in pond management intensity, from actively managed to unmanaged ponds, likely affects the types of plants that establish and persist either directly by manipulating the plant community or indirectly via effects of management on pond soil and water chemistry (e.g., Sinclair et al., 2020). For example, we expect that active management will favor invasive plants with traits that can withstand frequent disturbance (e.g., Lososová et al., 2006), while unmanaged pond communities do not experience management-based disturbance, often for decades, likely favoring invaders that are less disturbance tolerant but are better competitors.

2. Methods

2.1. Study region

We performed this study in stormwater ponds within the urbanized area of Gainesville, FL, USA. Florida's combination of rapid urbanization, flat topography, and sub-tropical to tropical climate produces a high risk of urban flooding and thus high usage of stormwater ponds. The urbanized area of Gainesville encompasses about 740 stormwater ponds, and within-city heterogeneity in soil drainage and socioeconomics has produced a variety of dry, wet, actively managed and unmanaged ponds (Fig. 1).

2.2. Stormwater pond plant survey

We surveyed the presence of invasive plant species in 15 dry and 15 wet stormwater ponds (hereafter referred to as the pond 'type' treatment; $N = 30$) in July and August 2018. Sampling during peak biomass in Florida's subtropical climate mid- to late-summer ensured that the majority of invasive species were detectable if present. Dry and wet ponds were further divided into 'low' ($n = 5$), 'medium' ($n = 5$) and 'high' ($n = 5$) management categories (the 'management' treatment). Management categories were determined using an ordinal scoring system from 0 to 3 applied to both the upland and aquatic (temporarily or permanently inundated) sections of the ponds and were informed by satellite maps, visual observations and interviews with pond managers. Pond sections left unmanaged, identifiable by overgrown vegetation and woody debris, were scored as 0. Sections managed approximately once per year, which can involve mowing, debris clearance, and removal of drain blockages, were scored as 1. Sections consistently managed on a monthly, seasonal, or as needed basis, were scored as 2. Sections consistently managed and with purposeful plantings were scored as 3. 'Low' management ponds received a total score across sections of 0–1, 'Medium' from 2 to 3, and 'High' from 4 to 5.

In addition to capturing differences in management intensity, the survey was designed to control for the influences of pond spatial associations, age (i.e., year of construction), area and depth on the invasive plant community. We ensured all sampled ponds were located in different residential, commercial or industrial areas within the city to minimize the potential for spatial relationships. We also ensured that the construction years of sampled ponds evenly spanned the decades from 1980 to 2010 within each treatment level (i.e., wet and dry and low, medium, and high management), and that the area of all surveyed ponds was < 0.01 km^2. Sampled ponds also tended to be shallow (depth 1.7 ± 1.2 m; mean $\pm$ SD), and at the time of sampling consisted of mostly acidic soils and sediments (pH of 6.73 ± 0.73 and 6.64 ± 0.65 respectively). Further details on pond characteristics can be found in Appendix A, and further details on survey design can be found in Sinclair et al. (2020). Initial statistical analyses (detailed in Appendix B) revealed no effects of inter-pond distance, age, area or depth on invasive plant trait composition, enabling us to exclude these factors from analyses of pond type and management level.

Each pond was surveyed in its entirety for plant species that have been classified as invasive or potentially invasive in Florida by the Florida Exotic Pest Plant Council (www.fleppc.org) and the US Department of Agriculture. We identified a total of 28 of these species across our 30 sampled ponds (see Appendix C: Table C1 for species names and pond occurrences; see Sinclair et al., 2020 for information on invasive plant species richness and cover).

2.3. Invasive plant traits

Using our species list of 28 pond invaders, we mined the primary literature and existing databases (e.g., Centre for Agriculture and Bioscience International, TRY, USDA) for data on plant functional traits, which were compiled into a database of 40 total traits (Table 1 and Appendix D: Table D1). Functional traits were grouped into four broad categories that relate to how each plant may have arrived or survived in stormwater ponds: (1) dispersal, (2) life history, (3) morphology and (4) physiology. Individual traits were included based on their relevance to these categories and if data was available for > 70% of our detected invasives. Eight traits had missing data (shown in Table 1), most of which was due to the trait not applying to the species at all or in Florida (e.g., disturbed soil tolerance for floating aquatic plants). Some traits were excluded from further analysis if they strongly correlated with other traits or if a categorical trait had too much variability among species to create meaningful groupings. These two conditions respectively only applied to minimum leaf length and width which correlated strongly to their maximums ($r = 0.96$ and $r = 0.95$ respectively), and leaf shape which had unique values for five out of 28 species and three additional shape values shared by only two species (Table 1). Following this trait exclusion process, 37 total traits remained for analyses. Average trait values were used for species that had multiple recorded values for a given numeric trait (e.g., seed weight obtained from the TRY database; Kattge, Díaz, & Lavorel, 2011; Appendix E).

In addition to plant functional traits, we also gathered information on the likely continent of origin of each species, whether the species was purposefully or accidentally introduced to Florida, the reason if intentionally introduced, and whether the species was or is commercially sold in Florida ('human-related' traits; Table 1 and Appendix D: Table D1). The initial origins, pathways, and history of biological invasions are often anecdotal or difficult to verify, and we therefore did not use these four additional human-related traits in any formal analysis. However, the history of human-mediated introduction can be useful as a qualitative assessment of which types of invasive plants tend to colonize a habitat, the pathways through which these invasions may have occurred, and determining which invasion pathways and plant types to target for control efforts.

2.4. Common traits

We quantified which of the 37 functional traits were common across our plant invaders (Objective 1) separately for categorical/binary and discrete/continuous numeric traits. Any categorical or binary trait for which > 70% of our species (i.e., 20 out of 28) shared a single trait value was considered common. For numeric traits, we assessed commonality based on the width of the range between the 1st and 3rd data quartiles using trait values scaled to their means and two standard deviations. This rescaling allowed for comparison of variability among traits measured with different units. We also used violin plots, in combination with interquartile ranges, to visually assess whether the data for each species' discrete/continuous numeric traits tended to cluster around particular values.

2.5. Effects of pond type and management on trait composition

To determine whether pond trait composition changed based on pond type, management intensity, or their interaction (Objective 2), we used similar multivariate ordination procedures as those recommended or used for studying community trait composition by Laliberté and Legendre (2010) and Nunez-Mir, Guo, Rejmánek, Iannone, and Fei (2019), as further summarized in Fig. 2. Of the 37 total invasive plant traits, five were excluded from these analyses because they had little to no variation among species (common to 93–100% of species; reported below in our results and Table 1) and therefore could exhibit little to no response to differences in pond type or management. Data on the remaining 32 functional traits (columns) of the 28 invasive plant species (rows) was converted to a dissimilarity matrix using Gower's distance, a distance measure that can incorporate mixed data types (i.e., numeric, categorical and ordinal trait data), and can handle some missing values (Gower, 1971; Nunez-Mir et al., 2019; Pavoine, Vallet, Dufour, Gachet,

Table 1
Functional and human-related trait categories and traits for the 28 species of stormwater pond invasive plants in the traits database. Further detail on how each was quantitatively or qualitatively assessed is provided in Appendix D: Table D1.

Dispersal	Animal dispersal		Minimum leaf width[3]
	Bird dispersal		Primary growth form
	Gravity dispersal		Seed mass[2]
	Water dispersal		Tissue type
	Wind dispersal	**Physiology**	Allelopathy
Life history	Asexual regeneration[1]		Chromosome number
	Cotyledon type		Disturbed soil tolerance[1,2]
	Growth rate		Drought tolerance
	Leaf longevity		Fire tolerance
	Plant longevity[1]		Flood tolerance
	Seed dormancy[2]		Maximum hardiness zone
	Self-pollination[2]		Minimum hardiness zone
	Sexual regeneration		Maximum pH tolerance
Morphology	Flower color number[2]		Minimum pH tolerance[1]
	Flower type[2]		Maximum shade tolerance
	Fruit type		Maximum sun tolerance[1]
	Leaf arrangement		Photosynthetic method
	Leaf shape[3]		Salinity tolerance
	Leaf type	**Human-related**	Continent of origin
	Maximum leaf length		Initial introduction
	Maximum leaf width		Reason for introduction[2]
	Minimum leaf length[3]		Commercially sold in Florida

[1] Traits not included in multivariate models due to lack of variance among species.
[2] Traits with missing values.
[3] Traits not included in any analyses due to too much variability among species or highly correlated to other traits.

& Daniel, 2009). All ordinal traits were transformed to ranks following Podani (1999). The contribution of each trait to producing the Gower distance matrix was also weighted based on the number of traits in each of our four major trait categories. This adjustment ensured that the overall trait categories of dispersal, life history, morphology and physiology each contributed equally to estimated species dissimilarities because each is subdivided into different numbers of traits (Laliberté & Legendre, 2010).

Distances among species within the resulting Gower distance matrix represent their degree of trait similarity, with shorter distances indicating species with more similar values across their functional traits. We analysed these species trait dissimilarities with Principal Coordinate Analysis (PCoA; Fig. 2b) after Cailliez transformation (Cailliez, 1983). This transformation is necessary to convert a non-Euclidean distance matrix to a Euclidean one, allowing the use of Euclidean multivariate analyses, such as Redundancy Analysis (RDA).

Average invasive plant trait composition for each stormwater pond was then calculated as the centroid of each species location across all PCoA axes for the subgroup of species present within each pond (Laliberté & Legendre, 2010). As an example, if invasive plant species

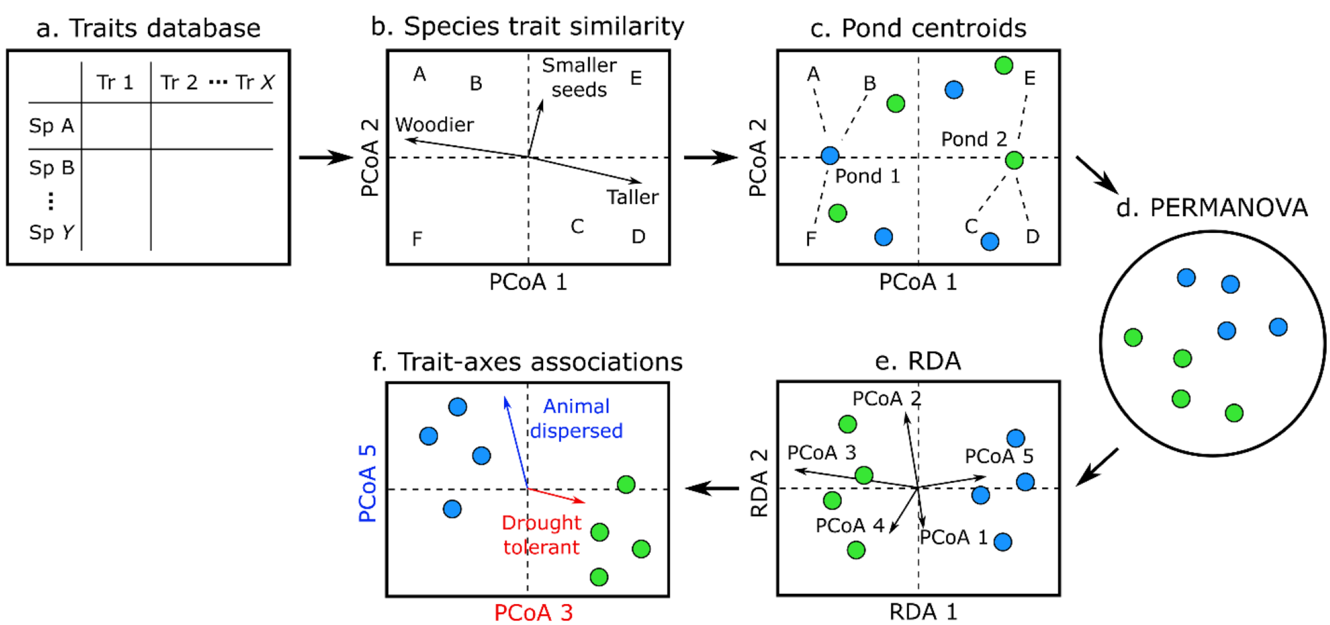

Fig. 2. Statistical methods used to determine effects of stormwater pond type and management on trait composition. (a to b) PCoA ordination of the traits database quantified trait similarities among plant species. (c) Pond trait composition was then calculated as the centroid across all PCoA axes of the species present in each pond (points in panel c are ponds and their colors depict different hypothetical treatment levels, e.g., dry vs. wet). For example, only species A, B and F are present in Pond 1, while species C, D, and E are present in Pond 2. (d) A PERMANOVA determines if pond centroid positions differ relative to treatment levels (illustrated with green versus blue point colors). If the PERMANOVA detects a difference between categories then (e) an RDA determines which PCoA axes best relate to these differences (PCoA 3 and 5 in the example). (f) We then determine which traits correlate to the important PCoA axes revealed in (e). Only those traits correlated at the $P < 0.05$ level are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

A, B and F are present in a pond (Fig. 2c), then overall average pond trait composition is the centroid of the combined A, B and F positions in the PCoA. Single species positions were used as centroids in instances where only a single invasive plant was found in a pond. One dry, high management pond out of the 30 total surveyed was excluded because it was uninvaded, thus $N = 29$ for the total number of pond centroids and further analyses using these centroids.

A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was then used to determine whether pond centroid positions (i.e., average trait composition) significantly differed ($P < 0.05$) between pond type and/or management categories (Fig. 2d). The Euclidean distance matrix of pond centroid locations across all trait PCoA axes was the multivariate response variable for this model and predictors were the categorical variables for pond type (dry or wet) and management intensity (low, medium and high), along with their interaction (Pond trait composition ~type*management).

RDA was then used to identify which PCoA axes most strongly related to any significant differences among pond categories revealed by the PERMANOVA (Fig. 2e). Pond centroid positions across the first seven PCoA axes (the major axes that each explain > 5% of trait variation, representing 70.1% total variation) were used as the multivariate response variables, with only the significant pond type and/or management effects identified by the PERMANOVA as constraining predictors. Only traits that significantly related (based on Pearson's r; $P < 0.05$) to the PCoA axes that best captured differences detected by the PERMANOVA, i.e. axes with the highest RDA loadings, were examined (Fig. 2f). Combined, the PERMANOVA determines the magnitude and significance of any individual or interactive effects of pond type and management on pond trait composition, while the RDA acts as a guide to which PCoA axes and thus traits were primarily associated with any detected effects.

All multivariate analyses were performed in R 3.5.0 (R Core Team, 2018). The 'FD' package (v1.0–12; Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2014) was used to produce the Gower's distance matrix, the 'ape' package (v5.2; Paradis & Schliep, 2018) was used to create the PCoA, and the 'vegan' package (v2.5-2; Oksanen, Guillaume Blanchet, Friendly, Kindt, Legendre, McGlinn, Minchin, O'Hara, Simpson, Solymos, Stevens, Szoecs, & Wagner, 2018) was used to perform the PERMANOVA, RDA and Mantel correlogram (Appendix B) analyses.

3. Results

3.1. Common traits

Values for five categorical functional traits were the same across all, or close to all, of the 28 detected invasive plant species (Fig. 3; as stated above these variables were excluded from the PCoA trait analysis). All 28 invasive plant species were tolerant of acidic soils and all 26 species that can grow in soil (2 only grow as floating aquatic plants) were tolerant of disturbed soil conditions. All species were also perennials, and the majority of detected plant invaders can asexually regenerate (27/28 species or 96%) and were tolerant of full sun (93%).

In addition to the above-mentioned commonalities, we found numerous similarities among species in other categorical traits. Specifically, most species disperse via non-bird animal (78%; hereafter 'animal') and water (71%) vectors and are capable of rapid growth (78%) and sexual regeneration (75%). Leaf morphology was also generally consistent, with most species exhibiting simple leaves (78%). In terms of physiology, our invasive stormwater pond plants have similar photosynthetic methods (82% are C3) and are generally tolerant of drought (71% with medium or high drought tolerance) and flooding (71% with medium or high flood tolerance), but not full shade (71% of species are only tolerant of partial shade).

Among the seven numeric traits we estimated (Fig. 4), species maximum hardiness zone and seed mass exhibited the least variability. These two traits exhibited the narrowest interquartile ranges (0.16 and 0.29 respectively) in their scaled values, with data points clustering respectively around a median hardiness zone of 11 and median seed mass of 5.9 g (Fig. 4a and b). In contrast, the other numeric traits were more variable. Their scaled interquartile ranges were comparatively wider (0.39–0.69), with data points less clustered around particular values (Fig. 4c–g).

There were also commonalities among our 28 plant invaders in their human-related traits. The majority of invaders originated from Asia (68%) or South America (25%) and were initially purposefully (89%) rather than accidentally introduced to Florida. Most species have a history of introduction for horticultural purposes (75%), specifically 18 species used in landscaping and 3 in aquariums or decorative ponds, while fewer species (43%) have been introduced for food and/or agricultural purposes. Note that species percentages for the specific purposes of introduction can sum to > 100% because some species were introduced for both horticultural and agricultural purposes. Of our 28 invaders, a majority (86%) have at some point been available for purchase in Florida and 10 of these species (36%), as of 2019, were still being sold for ornamental use.

3.2. Influence of pond type and management on trait composition

About 20% of the total variation in pond invasive plant trait composition was explained by management intensity (low, medium and high; PERMANOVA; $R^2 = 0.20$, F $\text{model}_{2,28} = 3.2$, $P = 0.0017$), with no evidence for effects of pond type (dry versus wet; PERMANOVA; $R^2 = 0.037$, F $\text{model}_{1,28} = 1.2$, $P = 0.26$), nor interactive effects between pond type and management (type*management; PERMANOVA; $R^2 = 0.061$, F $\text{model}_{2,28} = 1.0$, $P = 0.42$). Based on our post-hoc RDA, PCoA axes 2 and 4 best related to management-driven shifts in pond trait composition (Appendix F: Fig. F1), together capturing 22.7% of total trait variation (14.1% on PCoA 2 and 8.6% on PCoA 4) and thus likely most of the management effect on trait composition. PCoA axis 2 was significantly related to traits for gravity dispersal, seed dormancy, sexual regeneration, cotyledon type, primary growth form, tissue type, drought tolerance and maximum pH tolerance (black and red arrows in Fig. 5), and captured shifts in these traits as management intensity increased from low to medium to high (moving from left to right in Fig. 5a). PCoA axis 4 was significantly related to traits for animal dispersal, cotyledon type, leaf longevity, leaf arrangement and flower type (blue and red arrows in Fig. 4), and captured shifts in these traits between both low and medium management ponds compared to high management ponds (moving top to bottom in Fig. 5a). The individual plant species associated with the above trait relationships to PCoA axes 2 and 4 are shown in Appendix G: Fig. G1.

4. Discussion

4.1. Common traits

Despite heterogeneity in the design and management of our surveyed ponds, we found broad homogeneities in plant functional traits that suggest two general mechanisms filtering the species present in these designed ecosystems: (1) human interests in species serving needs such as aesthetics and food; and (2) the ability to disperse to and establish in unique urban ecosystems. These two mechanisms are in agreement with published frameworks outlining general rules for urban community assembly (Aronson et al., 2016; Williams et al., 2009) and with other studies of the general mechanisms that determine plant trait composition in urban areas (e.g., Kendal et al., 2012; Pataki, McCarthy, Gillespie, Jenerette, & Pincetl, 2013; Johnson, Borowy, & Swan, 2018).

Regarding plant selection for human interests, most of our pond invaders (89%) were purposefully introduced to Florida for horticulture or agriculture. This result highlights the role of these enterprises in shaping the composition of the urban plant species pool available to

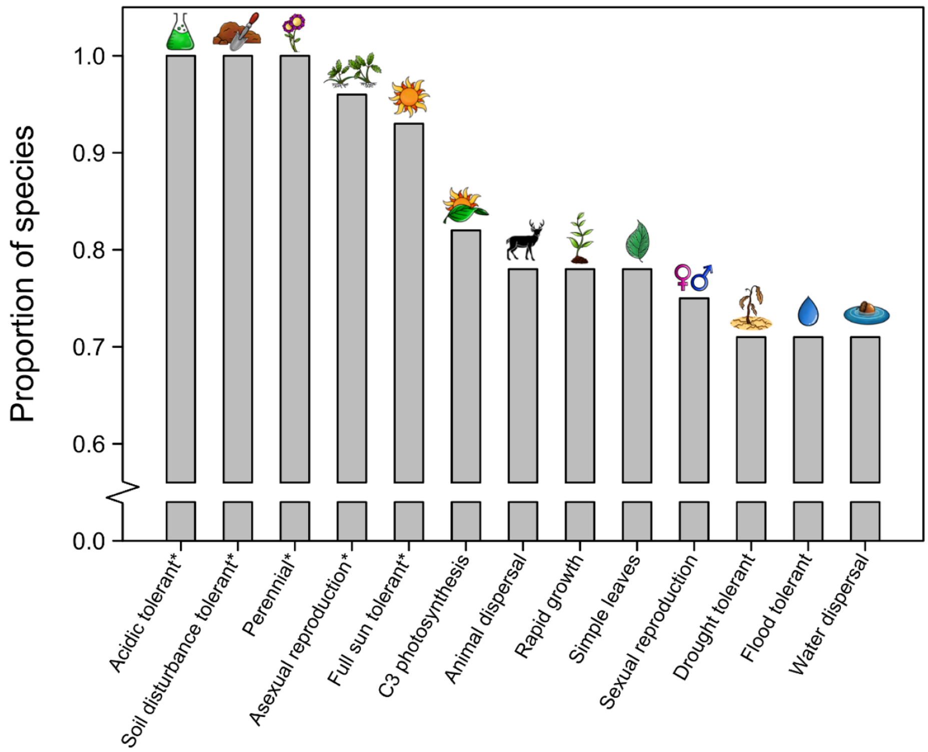

Fig. 3. Traits shared by > 70% of invasive stormwater pond plants. Note the break in the y-axis, and that traits listed as "Drought tolerant" and "Flood tolerant" include species classified as either medium or highly tolerant. Trait labels with '*' indicate traits excluded from multivariate models due to lack of variability among species.

colonize newly manufactured ecosystems (i.e., greater purposeful introduction effort by people drives colonization; Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007). Plants introduced to serve human interests are not a random subset of global flora because they typically possess desirable traits. For example, we found a prevalence of perennials that can asexually regenerate, which can be desirable plant traits for home gardeners (Hodkinson & Thompson, 1997; Lowenstein & Minor, 2016). It is therefore not surprising that the mostly horticultural and to a lesser degree agricultural plants (75% and 43% of species respectively) that colonized our surveyed ecosystems shared traits potentially related to urban usage, including rapid growth and poor tolerance of full shade (Martin, Canham, & Marks, 2009). Broad commonalities in the traits of purposefully introduced plants can also occur when species are obtained from the same source regions, primarily Asia and South America for the species we found, due to shared phylogenetic histories or environmental similarities (e.g., similarities in traits for leaf shape or size; Pataki et al., 2013).

While horticulture and agriculture clearly formed the colonist pool of stormwater pond invaders, so too did a species' ability to arrive and survive in stormwater ponds. Our stormwater pond species tended to be generally tolerant of acidic conditions, which matched the more neutral to acidic soils and sediments of our ponds. Similarly, commonalities in plant tolerance for both drought and flooding may relate to the need to withstand the stresses of the dynamic hydrology of stormwater systems. However, it was difficult to assign many of our shared plant traits to either mechanisms of human interests or urban establishment. For example, species commonalities in environmental tolerances, hardiness, asexual regeneration and small seeds can occur due to human plant preferences (Hodkinson & Thompson, 1997; Kendal et al., 2012; Martin et al., 2009), which we found can likely determine the pool of plants available to colonize stormwater ponds. Similarly, pond invader commonalities in animal/water dispersal could be indicative of human selection in the surrounding landscape for horticultural or agricultural plants with fleshy fruit (Herrera, 2002). Alternatively, these same trait commonalities could be a result of the types of plants that can successfully disperse to (e.g., small seeds or water dispersal), survive within (e.g., hardiness zone and sun tolerance), and reproduce (e.g., asexual regeneration) in stormwater ponds. Disentangling which trait commonalities are driven by human selection in the urban landscape around stormwater ponds, which traits are necessary for establishing in these designed ecosystems, and which traits relate to both mechanisms is a fruitful avenue for future research.

There were differences between the traits of the pond colonists in our study system versus those identified for urban areas in general, highlighting the need to uncover the factors driving trait differences among different urban ecosystem types. An example is the universal prevalence of perennialism across the stormwater pond colonizers we found, while other studies often report urban colonizers to be primarily comprised of annuals as these plants tend to establish better in disturbed habitats (Bertoncini et al., 2012; Palma et al., 2017; Zeeman et al., 2017). Additionally, all species were tolerant of acidic soil conditions while fewer (64%) were tolerant of alkaline conditions. This pattern contrasts to the tolerance of alkaline conditions often found in the traits of urban flora, ascribed to the need to tolerate built environments which tend towards a more basic pH (Thompson & McCarthy, 2008; Williams et al., 2015). However, as discussed in the introduction, urban areas can be highly heterogeneous. Traits determined to drive urban plant establishment across a city may not apply to smaller spatial scales or to a given subset of ecosystems. Cities generally exhibit high impervious surface cover (McKinney, 2002), which may favor annual plants tolerant of alkaline conditions, but the designed ecosystems within a city are not necessarily paved and disturbed to the same degree. Urban ecosystems, like our stormwater ponds, with available water, soil resources and a mixture of managed and undisturbed habitats with less densely built-up area could be more favorable to perennials (Lososová et al., 2006) and plants with lower alkalinity tolerance (Godefroid & Koedam, 2007). While there are likely large-scale trait filtering processes that operate across urban systems,

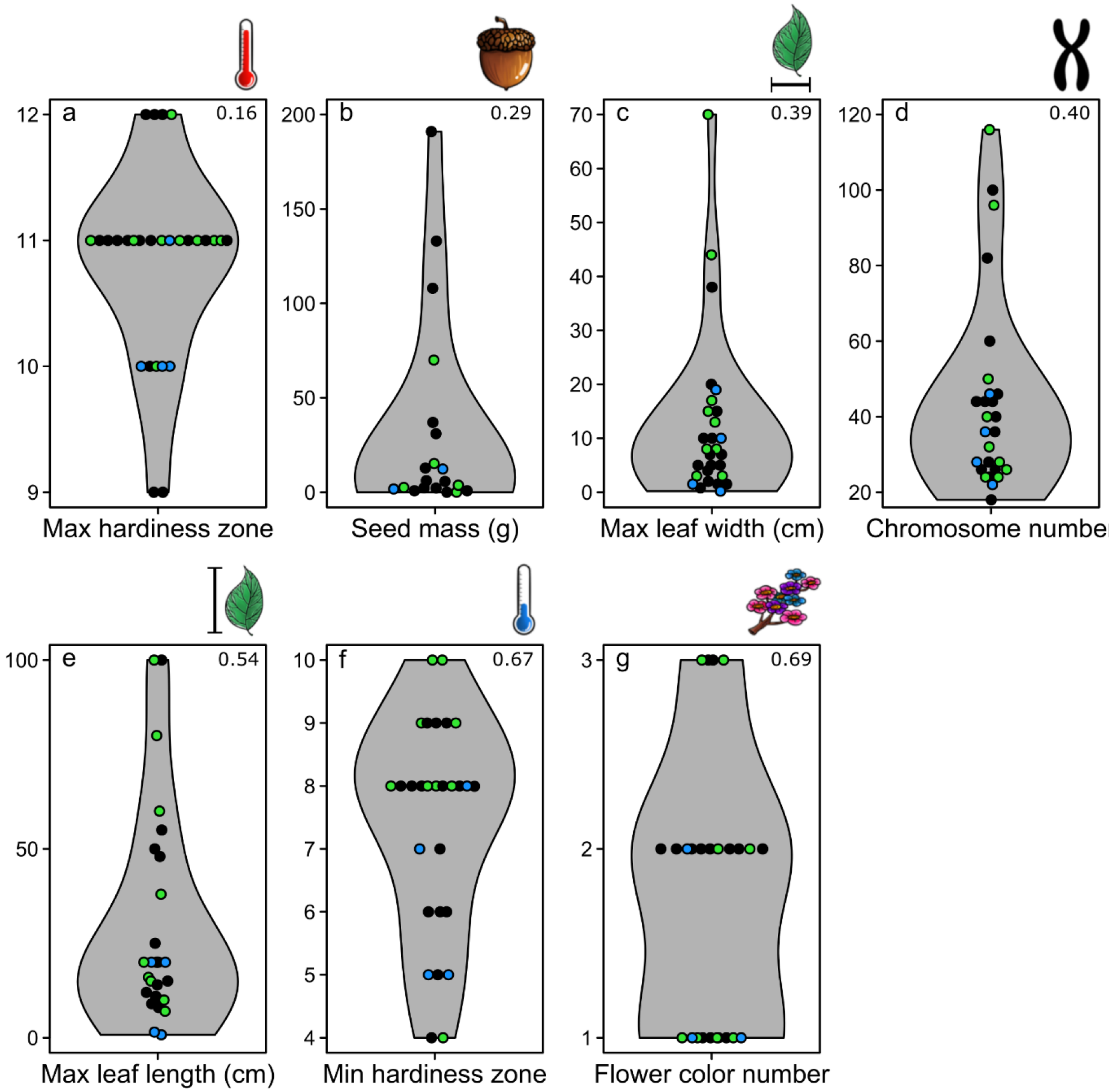

Fig. 4. Values (points) and data probability density distributions (violin plots) of numeric traits for invasive stormwater pond plants. Traits are ordered by the coefficient of variation (top right corner of each panel) of their scaled values across species, thus (a–g) respectively show the least to the most variable traits. Point colors represent trait values for species detected in both dry and wet ponds (black), dry ponds only (green), and wet ponds only (blue).

which can be identified by examining traits of all urban flora, smaller-scale research such as ours in specific urban ecosystems is also needed to establish how general plant filtering mechanisms may change across heterogeneous urban habitat types.

4.2. Influence of pond type and management on trait composition

Although we detected broad trait similarities among stormwater pond plant invaders, trait composition still responded to changes in management intensity (we found no such effects for pond type). In general, low management ponds (dry or wet) tended to be comprised of woodier invasive plants (i.e., trees and shrubs) with other traits associated with the types of woody invaders we found, primarily dicots that can sexually regenerate, that exhibit higher tolerances to drought and alkaline conditions, and with gravity dispersed seeds capable of dormancy. As management intensity increased from low to medium to high, ponds tended to become comprised of more herbaceous invaders, such as forbs and ferns (Fig. 5d), with other traits associated with the identified species of herbaceous pond invaders, such as lower tolerances to drought and alkalinity. The trait composition of high management ponds was also different compared to both low and medium management ponds, with high management ponds specifically characterized by more animal dispersed, dioecious species.

These management-driven shifts in plant trait composition are suggestive of successional differences among our surveyed designed ecosystems, which we expected as urban plant succession is strongly influenced by management and land disturbance (Del Tredici, 2010). Compositional differences among ponds in plant traits were largely in agreement with our initial expectations that low management communities might be more structured by competition, represented by a woodier, later stage successional community, while higher management communities may be more structured by disturbance, represented

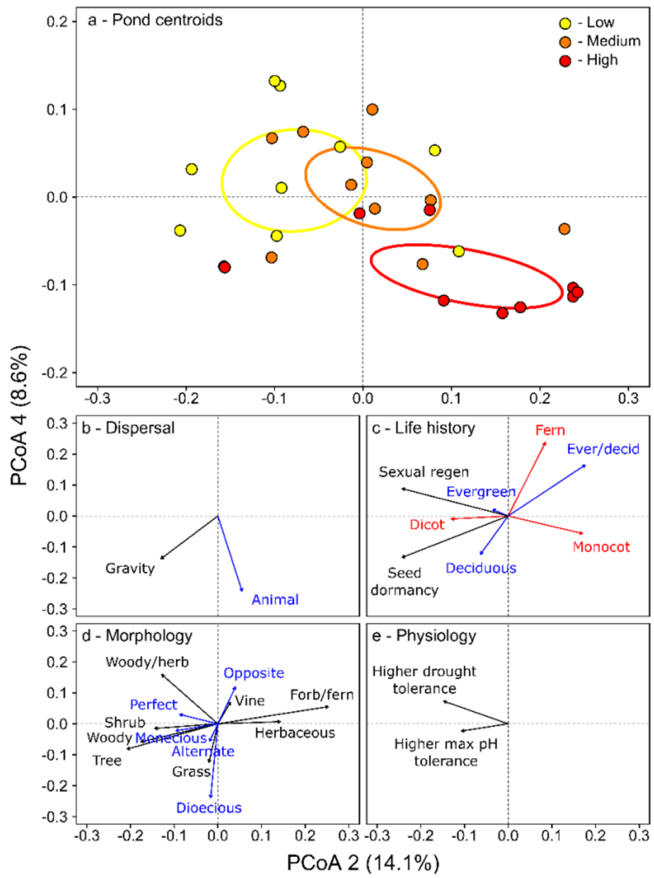

Fig. 5. Management-driven shifts in invasive stormwater pond plant trait composition (we found no effect of pond type). Ordinations depict (a) management-driven shifts in average pond plant trait composition and (b–e) trait associations with PCoA 2 and 4, the axes over which separation among management levels occurred. In (a), filled circles represent the average trait composition (pond centroids) for the invasive plant community present in each pond at each management intensity (Low = yellow; Medium = orange; High = red). In (b–e), arrows are present only for traits significantly associated to PCoA 2 or 4, with longer arrows closer to an axis depicting a stronger correlation. Black arrows and text represent traits significantly correlated only to PCoA 2, blue coloration represents significant correlations only to PCoA 4, and red coloration represents significant correlations to both axes.

by a more herbaceous, earlier successional community. Less managed stormwater ponds represent habitat that was built, sometimes several decades ago, then effectively abandoned or minimally maintained, allowing succession to proceed uninterrupted. Conversely, the communities of high management ponds, all of which were built at least a decade ago, are continually reset in successional time through cutting back and removal of unwanted or disruptive vegetation. This style of active ecosystem management may therefore adjust the environmental filters that plants are exposed to in urban areas by selecting for species that can quickly re-colonize after removal or capitalize on gaps opened by frequent disturbance. The strong trait filter imposed by management was further evidenced by the fact that *Alternanthera philoxeroides* (Alligator weed) was the most characteristic invader of highly managed stormwater ponds, occupying 70% of high management ponds compared to 30% and 40% of low and medium managed habitats (Appendix C: Table C1). This species is an amphibious, prohibited aquatic plant in Florida which cannot be possessed, collected, transported, cultivated or imported due to its highly invasive capabilities. Alligator weed is capable of rapid growth, it is tolerant of disturbance, and is a hardy colonizer of aquatic and semi-aquatic habitats, highlighting the kinds of traits necessary to colonize highly managed stormwater pond ecosystems.

Trait compositional shifts related to changes in management intensity showed possible evidence of a unique role for animal dispersal in actively managed stormwater ponds. While the capability to disperse via animal vectors was a trait shared by most species (78%), the species incapable of utilizing animal vectors never occurred in highly managed ponds, suggesting animal dispersal may be a key trait driving plant occurrence in these ecosystems. The strong association of animal dispersal with highly managed ponds may not have occurred specifically due to animal-mediated dispersal, but instead from greater usage of horticultural plants with fleshy fruit in more manicured urban areas (i.e., human-use drives this trait association). However, it is unlikely that horticulture was the source of these animal-dispersed invaders because the plants capable of animal dispersal that were found in highly managed ponds (Appendix G: Fig. G1) included several species that are not associated with horticulture or the production of fleshy fruit, such as species with small seeds and vegetative fragments that can disperse attached to animals. Therefore, a more likely explanation is that actively managed ponds may be more attractive or accessible to animals (e.g., some frog species prefer actively managed pond vegetation; McCarthy & Lathrop, 2011), or to visiting people carrying plant seeds on clothing. By attracting animal or human vectors, highly managed stormwater ponds may therefore act as stepping-stones across urban landscapes for the longer distance movement of animal-dispersed plants, which could play a role both in improving connectivity and spreading invaders.

4.3. Practical implications

Our results show that there is a consistent type of invasive plant associated with stormwater ponds in general and that these traits vary across management regimes. The invaders we found originated from purposeful introductions for urban horticultural and to a lesser degree agricultural use, and can successfully colonize the unique environment of stormwater ponds. Limiting invader planting and establishment in surrounding gardens, parks, yards, lawns, and decorative ponds, for example through removal programs and greater emphasis on native horticultural plant use, will serve to reduce both urban invasions in general and subsequent colonization and spread into designed ecosystems. Additionally, the flora of stormwater ponds could be further manipulated to improve both engineered and ecological function through the planting of a diversity of non-harmful native and non-native species that could improve resistance to future invasion. However, the broad presence of perennial and asexual invaders is also a cause for concern since eradication of these invaders may require repeated attempts. Furthermore, management activities that directly control or remove pond invaders must be careful to avoid methods that could promote re-invasion or the establishment of new invaders via disturbance, changes in resource availability, non-target effects on natives and introduction of other invasive plant propagules.

In terms of management-driven trait shifts, control programs started for less managed ponds should focus on identification and removal of woody invaders and should employ methods to prevent regeneration (e.g., treating tree stumps). Less managed ponds may also have more persistent invader seed banks because they tend to harbor invaders that exhibit seed dormancy (Fig. 5c), necessitating repeated monitoring to prevent re-invasion. For actively managed ponds, invader control should target herbaceous species, such as through the use of herbicides approved for aquatic habitats, and should focus on areas where these plant invaders will tend to occur to reduce cost and chemical usage, such as disturbed or less managed sections around the water's edge that are more readily colonized.

5. Conclusions

Our study shows that there can be commonalities in the traits of plants that colonize and invade particular designed ecosystems, as evidenced by five traits broadly shared across the 28 invasive plant species that we found in our 30 surveyed stormwater ponds. Identifying these common traits improves our understanding of the general drivers of plant establishment in designed ecosystems, and improves invasive plant management by informing of likely invasion pathways and the types of plants to target for control. For instance, in the stormwater ponds of our study region, we found that horticulture is a key invasion pathway to manage and that control will need to target perennial plants having asexual and/or multiple forms of reproduction. Additionally, the shift from more disturbance-tolerant to competitive invasive plants that we found in relation to increasing management intensity highlights the clear effects of urban plant management on the types of invasive plants that establish in stormwater ponds, and possibly other types of designed ecosystems. These trait shifts among different pond management intensities also inform how and where to focus invasive plant control, such as the need to identify and manage herbaceous versus woody invaders in actively managed versus less consistently managed pond communities.

Importantly, we found inconsistencies between common traits of stormwater pond plant invaders (i.e., acidic soil tolerance and perennialism) and those of urban flora in general (i.e., alkalinity tolerance and annualism). These differences reveal trait variability among the plant communities within cities, and thus the need for traits-based research across a variety of urban land cover and ecosystem types. Furthermore, it is important to determine whether the results from our study of invasive stormwater pond plants in central Florida can apply more broadly to other stormwater ponds being continually constructed in cities across the globe (which also harbor native plant species). We therefore need to know how our results vary geographically. That is, whether the common traits we identified are shared by stormwater pond plant invaders in other regions, and whether these traits are also shared by native pond plants. If so, we might predict species composition of stormwater ponds to be driven in part by horticultural choices in nearby urban landscapes. Finally, given the extensiveness and connectivity of stormwater pond networks, we need to determine the degree to which they promote the spread of invasive plants into natural areas, and the types of plant species (both native and non-native) that can disperse among the increasing number of ponds in urban landscapes. Filling in these knowledge gaps regarding the ecological role played by stormwater ponds can help to maximize the ecological benefits of these increasingly common designed ecosystems.

6. Data statement

Data is publicly available from the Institutional Repository at the University of Florida at https://ufdc.ufl.edu/IR00011151/00001.

CRediT authorship contribution statement

James S. Sinclair: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Carrie R. Adams:** Conceptualization, Methodology, Resources, Writing - review & editing, Funding acquisition. **Alexander J. Reisinger:** Conceptualization, Methodology, Resources, Writing - review & editing, Funding acquisition. **Eban Bean:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Lindsey S. Reisinger:** Conceptualization, Writing - review & editing. **Allyson L. Holmes:** Investigation, Data curation. **Basil V. Iannone:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Stormwater pond descriptions and locations

Table A1
Descriptive information and coordinates of all surveyed stormwater ponds. Rows are ordered by pond type (dry followed by wet ponds), then by pond management (low, medium then high), and then by year of construction from older to younger ponds. Also included is information on pond morphology and surrounding land use type. A map of pond locations is also provided in Fig. A1.

Pond	Latitude, Longitude	Type	Management	Year constructed	Surface area (m^2)	Max depth (m)	Surrounding urban land use type
1	29.683622, −82.316644	Dry	Low	1982	758.0	0.9	Commercial
2	29.648963, −82.413479	Dry	Low	1986	4264.1	1.8	High density housing
3	29.599844, −82.372418	Dry	Low	1991	1083.4	1.2	Commercial
4[a]	29.699566, −82.365998	Dry	Low	2005	2728.8	1.1	Institutional
5	29.622604, −82.375179	Dry	Low	2009	1183.9	2.0	Commercial
6[b]	29.611910, −82.374220	Dry	Medium	1984	6624.9	6.7	Industrial
7	29.668684, −82.319297	Dry	Medium	1996	783.6	0.3	Institutional
8	29.660486, −82.296576	Dry	Medium	1997	1468.2	0.8	Institutional
9	29.613863, −82.420927	Dry	Medium	2001	3375.5	3.6	Medium density housing
10	29.604007, −82.372506	Dry	Medium	2005	1044.9	1.2	Commercial
11	29.632854, −82.348365	Dry	High	1980	756.9	1.2	Institutional
12	29.609324, −82.373014	Dry	High	1991	2384.5	1.8	Institutional
13	29.600430, −82.419420	Dry	High	1996	2703.7	1.4	Commercial
14[c]	29.669295, −82.434306	Dry	High	1999	4350.6	1.2	High density housing
15	29.638407, −82.394912	Dry	High	2006	4481.1	0.6	High density housing
16[d]	29.636767, −82.348391	Wet	Low	1980	1440.0	2.4	Institutional
17	29.699200, −82.332940	Wet	Low	1988	4883.4	1.1	Light industrial
18	29.611900, −82.377370	Wet	Low	1994	2834.2	1.5	Industrial

(continued on next page)

Table A1 (*continued*)

Pond	Latitude, Longitude	Type	Management	Year constructed	Surface area (m^2)	Max depth (m)	Surrounding urban land use type
19	29.669007, −82.327055	Wet	Low	2001	1489.2	2.7	Institutional
20	29.700773, −82.344331	Wet	Low	2007	5514.7	3.3	Commercial
21	29.697381, −82.279818	Wet	Medium	1987	3330.8	2.1	Transportation
22	29.697347, −82.349865	Wet	Medium	1991	3417.3	0.9	Medium density housing
23[e]	29.660259, −82.445886	Wet	Medium	1994	2386.4	1.2	Institutional
24	29.704170, −82.337417	Wet	Medium	1996	507.1	2.3	Commercial
25	29.643205, −82.274135	Wet	Medium	2003	1335.8	0.6	High density housing
26	29.622477, −82.369161	Wet	High	1984	4893.7	0.6	High density housing
27	29.709746, −82.376417	Wet	High	1994	2719.4	1.2	High density housing
28[f]	29.691703, −82.398430	Wet	High	1996	4513.1	1.2	High density housing
29	29.643502, −82.297814	Wet	High	2001	1405.4	2.4	Medium density housing
30	29.706151, −82.344019	Wet	High	2006	1964.2	2.0	Commercial

[a–e]Ponds shown in the corresponding lettered panels of Fig. 1.

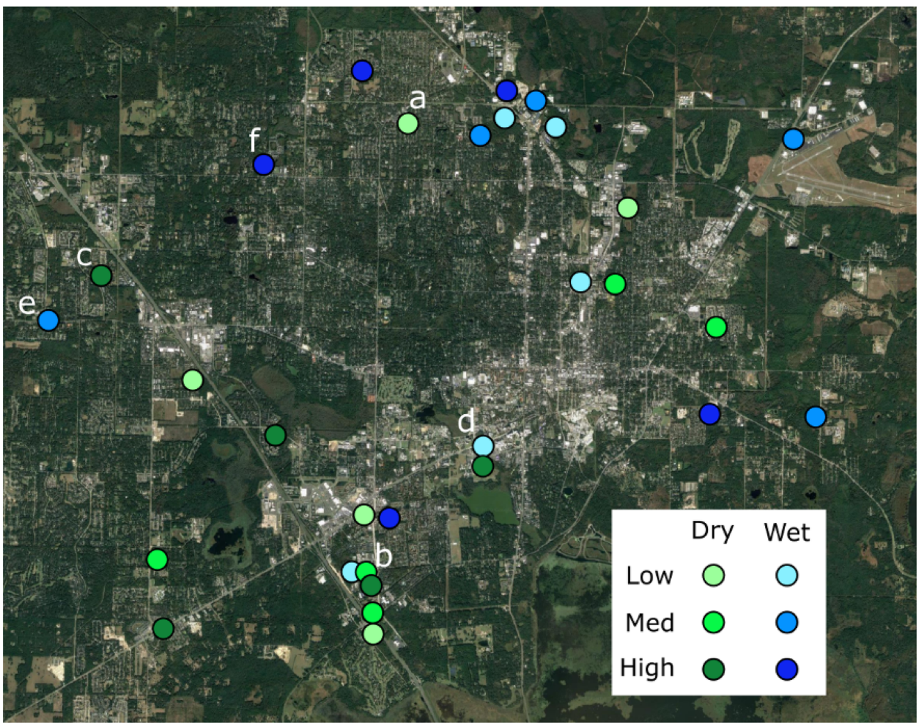

Fig. A1. Locations of 30 sampled stormwater ponds (circles) in Gainesville, FL, US. Management intensity is indicated by increasing point color darkness from lighter (low management) to darker (high management) coloration. Letters a–e represent the locations of the ponds shown in the corresponding lettered panels of Fig. 1 of the main research paper. Coordinates for all sampled ponds are listed in Appendix A: Table A1.

Appendix B. Influence of pond spatial proximity, age, area and depth

A Mantel correlogram and three PERMANOVAs were used to confirm that our study design successfully controlled for effects of pond spatial proximity, age, area and depth on plant trait composition. The Mantel correlogram (Oden & Sokal, 1986) determined if there was significant spatial autocorrelation in trait composition among ponds that were near to far distances from one another. This analysis used pond centroid locations across all trait PCoA axes as the multivariate response variable, with the spatial coordinates of each pond as the predictor representing geographic proximity (Pond trait composition ~ geographic position). We found no relationship between inter-pond distance and trait composition, evidenced by the lack of any significant spatial autocorrelation at all distance classes (Mantel correlogram; *P*-values of distance classes between 0.18 and 1.0).

The PERMANOVAs were used to determine whether variability in pond trait composition significantly related to pond age, area or depth. These analyses all used pond centroid locations across all trait PCoA axes as the response variable, and respectively pond year of construction (Pond trait composition ~ age), pond area (Pond trait composition ~ area) or pond depth (Pond trait composition ~ depth) as the predictor variables. We found no significant effects of either pond age, area or depth on trait composition. Differences in pond age only explained about 1.4% of trait variability among ponds (PERMANOVA; $R^2 = 0.014$, F $\text{model}_{1,28} = 0.4$, $P = 0.92$), area explained only 2.6% (PERMANOVA; $R^2 = 0.026$, F $\text{model}_{1,28} = 0.73$, $P = 0.61$), and depth explained only 1.9% (PERMANOVA; $R^2 = 0.019$, F $\text{model}_{1,28} = 0.53$, $P = 0.80$).

Appendix C. Invasive plant species found in the stormwater pond survey

Table C1

Taxonomy, growth form, likely origin and pond occurrences of all invasive plant species found in our stormwater pond survey. Species are ordered by their total number of occurrences across all 30 surveyed ponds (‘Total’) and then alphabetically by species name. Column headings ‘Primary growth form’ and ‘Continent of origin’ provide the values for each species for these traits, which are described in Appendix D: Table D1. Column headings ‘Dry’, ‘Wet’, ‘Low’, ‘Medium’ and ‘High’ refer to the number of unique occurrences for each species in dry versus wet ponds and in low, medium and high management ponds, respectively.

Family	Species	Common Name	Primary growth form	Continent of origin	Total	Dry	Wet	Low	Medium	High
Euphorbiaceae	*Triadica sebifera*	Chinese tallow	Tree	Asia	17	7	10	8	6	3
Amaranthaceae	*Alternanthera philoxeroides*	Alligator weed	Forb or herbaceous	South America	14	5	9	3	4	7
Verbenaceae	*Lantana camara*	Lantana	Shrub	South America	11	7	4	5	4	2
Oleaceae	*Ligustrum lucidum*	Glossy privet	Shrub	Asia	10	7	3	5	5	0
Fabaceae	*Albizia julibrissin*	Silk tree	Tree	Asia	7	5	2	4	2	1
Lauraceae	*Cinnamomum camphora*	Camphor tree	Tree	Asia	5	3	2	4	1	0
Sapindaceae	*Koelreuteria elegans*	Flamegold	Tree	Asia	5	5	0	3	2	0
Rubiaceae	*Paederia foetida*	Skunk vine	Vine	Asia	5	4	1	3	2	0
Myrsinaceae	*Ardisia crenata*	Coral ardisia	Shrub	Asia	4	3	1	3	1	0
Discoreaceae	*Dioscorea bulbifera*	Air potato	Vine	Asia	4	3	1	1	2	1
Araceae	*Landoltia punctata*	Spotted duckweed	Forb or herbaceous	Asia and Australia	4	0	4	1	2	1
Caprifoliaceae	*Lonicera japonica*	Japanese honeysuckle	Vine	Asia	4	2	2	2	2	0
Poaceae	*Paspalum urvillei*	Vasey's grass	Grass	Asia	4	2	2	1	2	1
Moraceae	*Broussonetia papyrifera*	Paper mulberry	Grass	Asia	3	2	1	0	2	1
Nephrolepidaceae	*Nephrolepis cordifolia*	Sword fern	Forb or herbaceous	Asia and Australia	3	2	1	1	2	0
Salviniaceae	*Salvinia minima*	Water spangles	Forb or herbaceous	South America	3	0	3	1	2	0
Araceae	*Colocasia esculenta*	Wild taro	Vine	Asia	2	1	1	0	1	1
Schizaeaceae	*Lygodium japonicum*	Japanese climbing fern	Vine	Asia and Australia	2	2	0	1	1	0
Poaceae	*Panicum repens*	Torpedo grass	Grass	Asia	2	1	1	1	0	1
Discoreaceae	*Dioscorea alata*	Winged yam	Vine	Asia	1	1	0	1	0	0
Onagraceae	*Ludwigia peruviana*	Peruvian primrosewillow	Forb or herbaceous	South America	1	1	0	1	0	0
Araceae	*Pistia stratiotes*	Water lettuce	Forb or herbaceous	Africa and South America	1	0	1	0	1	0
Fabaceae	*Pueraria montana*	Kudzu	Vine	Asia	1	0	1	0	1	0
Solanaceae	*Solanum viarum*	Tropical soda apple	Shrub	South America	1	1	0	1	0	0
Poaceae	*Sorghum halepense*	Johnson grass	Grass	Europe	1	1	0	0	1	0
Araceae	*Syngonium podophyllum*	Arrowhead vine	Vine	South America	1	1	0	1	0	0
Malvaceae	*Urena lobata*	Caesar's weed	Shrub	Asia	1	1	0	1	0	0
Araceae	*Xanthosoma sagittifolium*	Elephant ear	Forb or herbaceous	South America	1	1	0	1	0	0

Appendix D. List of plant functional traits

Table D1
Descriptions of all 40 plant functional traits and 4 human-related traits that comprise the trait database for the 28 invasive plant species identified across 30 stormwater ponds in Gainesville, FL, USA.

Trait category	Trait name	Description	Data type	Range of values
Dispersal	Animal dispersal	Use of non-bird, vertebrate animal vectors for seed dispersal	Binary	No (0), yes (1)
	Bird dispersal	Use of bird vectors for seed dispersal	Binary	No (0), yes (1)
	Gravity dispersal	Use of gravity for seed dispersal	Binary	No (0), yes (1)
	Water dispersal	Use of water for seed dispersal	Binary	No (0), yes (1)
	Wind dispersal	Use of wind for seed dispersal	Binary	No (0), yes (1)
Life history	Asexual regeneration	Species can vegetatively regenerate via bulbs, corms, fragments, layering, re-sprouting, rhizomes, runners, suckers or tubers in Florida	Binary	No (0), yes (1)
	Cotyledon type	Number of cotyledons	Categorical	Monocot, Dicot, Fern
	Growth rate	Speed of growth of which the species is capable	Ordinal	Slow, medium, rapid
	Leaf longevity	Leaf life cycle	Categorical	Evergreen, deciduous, evergreen/deciduous*
	Plant longevity	Plant life cycle	Categorical	Annual, perennial, annual/perennial**
	Seed dormancy	Species can produce dormant seeds	Binary	No (0), yes (1) or NA for species that do not produce seeds in Florida
	Self-pollination	Species is capable of self-pollination	Binary	No (0), yes (1) or NA if species does not pollinate in Florida
	Sexual regeneration	Species can sexually regenerate in Florida	Binary	No (0), yes (1)
Morphology	Flower color number	Number of flower colors species exhibits	Discrete numeric	0–3 or NA for species with no flowers in Florida
	Flower type	Type of flower	Categorical	Dioecious, monecious, perfect or NA for species with no flowers in Florida
	Fruit type	Type of fruit	Categorical	Aggregate, berry, capsule, caryopsis, drupe, legume, sporangia, syncarp, utricle
	Leaf arrangement	Arrangement of leaves	Categorical	Alternate, opposite
	Leaf shape	Shape of leaves	Categorical	Cordate, deltoid, elliptic, lanceolate, linear, oblong, obovate, orbicular, ovate, saggitate, spatulate
	Leaf type	Type of leaves	Categorical	Compound, simple, both
	Maximum leaf length	Higher range of leaf length	Continuous numeric	0.8–150 cm
	Maximum leaf width	Higher range of leaf width	Continuous numeric	0.2–70 cm
	Minimum leaf length	Lower range of leaf length	Continuous numeric	0.15–50 cm
	Minimum leaf width	Lower range of leaf width	Continuous numeric	0.15–40 cm
	Primary growth form	Primary growth form of each species	Categorical	Tree, shrub, vine, forb/fern, grass
	Seed mass	Mean species seed mass across TRY database records (see Appendix E for references)	Continuous numeric	0.02–191 mg or NA for species that do not produce seeds in Florida
	Tissue type	Type of plant tissue of species primary growth form	Categorical	Woody, herbaceous, woody/herbaceous***
Physiology	Allelopathy	Evidence from literature that species can exhibit allelopathy	Binary	No (0), yes (1)
	Chromosome number	Median number of sporophytic chromosomes	Discrete numeric	9–58
	Disturbed soil tolerance	Species tolerant of or preferring disturbed land	Binary	No (0), yes (1) or NA if species can only grow as a floating aquatic plant
	Drought tolerance	Species tolerance of drought conditions	Ordinal	Low, medium, high
	Fire tolerance	Species can tolerate fire	Binary	No (0), yes (1)
	Flood tolerance	Species tolerance of flood conditions	Ordinal	Low, medium, high
	Maximum hardiness zone	USDA species maximum hardiness zone	Discrete numeric	9–12
	Minimum hardiness zone	USDA species minimum hardiness zone	Discrete numeric	4–10
	Maximum pH tolerance	Higher range of species pH tolerance	Ordinal	Acidic, neutral, alkaline
	Minimum pH tolerance	Lower range of species pH tolerance	Ordinal	Acidic, neutral, alkaline
	Maximum shade tolerance	Species tolerance of shade	Ordinal	partial, full
	Maximum sun tolerance	Species tolerance of sun	Ordinal	partial, full

(*continued on next page*)

Table D1 (*continued*)

Trait category	Trait name	Description	Data type	Range of values
	Photosynthetic method	Species photosynthetic process	Categorical	C3, C4
	Salinity tolerance	Species tolerance of saline conditions	Ordinal	Low, medium, high
Human-related (not used in analyses)	Continent of origin	Initial source continent(s) of Florida species	Categorical	Asia, Africa, Australia, Europe, South America
	Initial introduction	Reason for species initial introduction to Florida	Categorical	Purposeful, accidental
	Reason for introduction	Reason species was introduced if introduction was purposeful	Categorical	Agriculture, horticulture or NA if introduction was accidental
	Commercially sold in Florida	Whether the species was or is commercially sold in Florida	Categorical	No, sold in past, presently sold

*Species is deciduous in cooler climates and evergreen in warmer climates.
**Species is annual in cooler and perennial in warmer climates.
***Herbaceous plants with tissues that harden over time to become somewhat woody.

Appendix E. TRY database sources for seed weight values

Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. van Groenendael, L. Klimes, J. Klimesova, S. Klotz, G. M. Rusch, Hermy, M., D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266-1274.

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Appendix F. PCoA axes associated with the effect of management

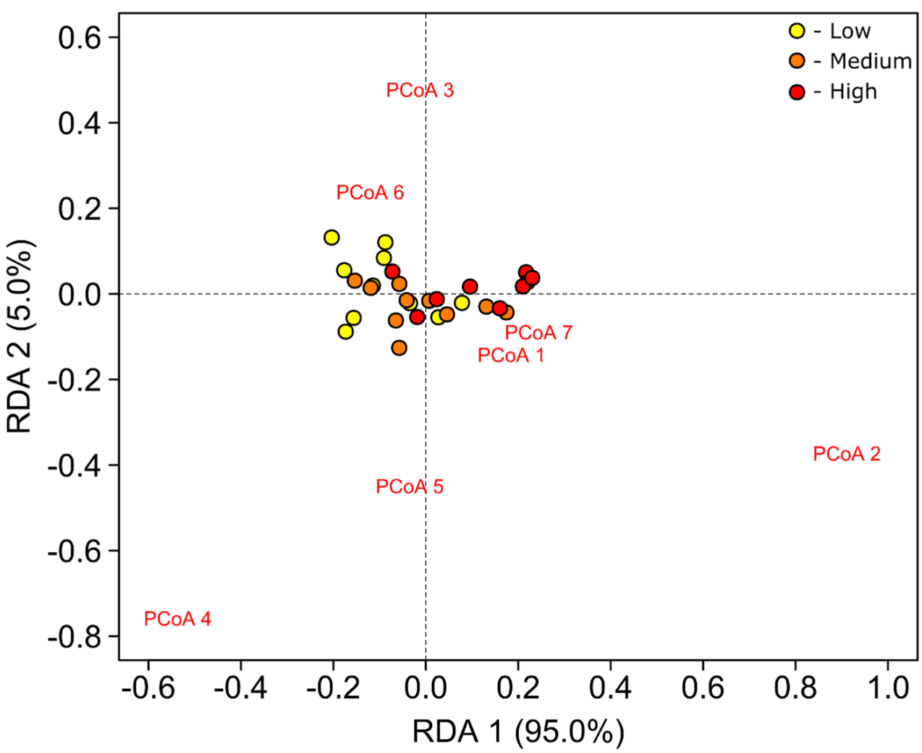

Fig. F1. Redundancy Analysis (RDA) of the relationship between pond centroid positions on the first seven trait Principal Coordinates Analysis (PCoA) axes (red text) constrained to pond management (Low = yellow; Medium = orange; High = red). Based on this analysis, RDA axis 1 almost entirely captures the relationship between trait composition and management (95%), with PCoA axes 2 and 4 most strongly loading onto this RDA axis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Appendix G. Species associations with PCoA axes 2 and 4

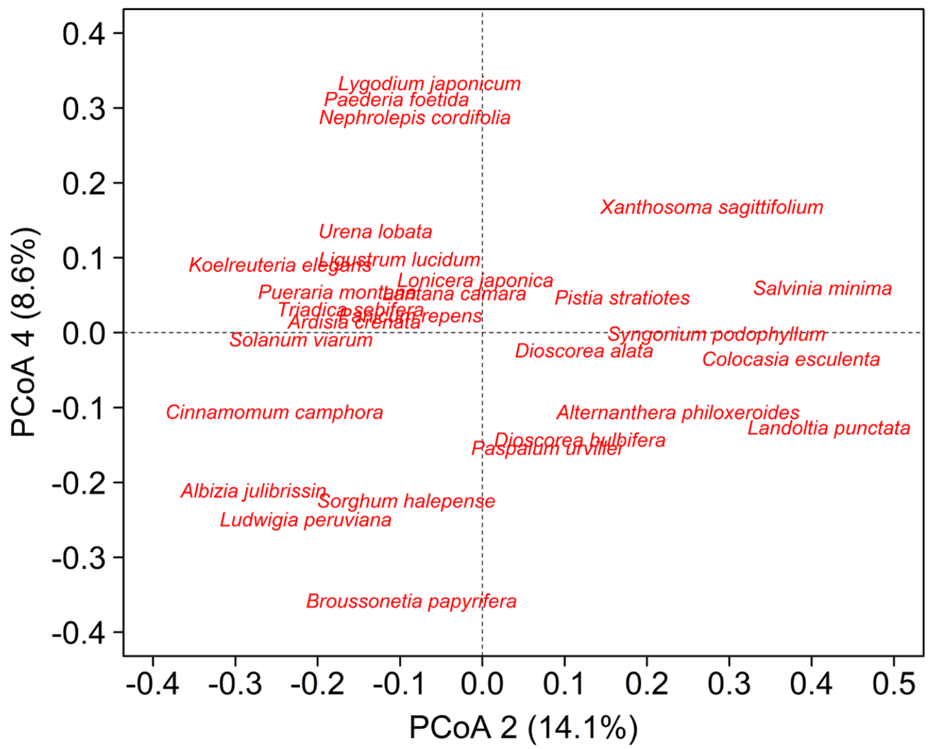

Fig. G1. Position of each invasive plant found within surveyed stormwater ponds along Principal Coordinates Analysis (PCoA) axes 2 and 4, the major axes related to management-driven variation in pond trait composition (as shown in Appendix F: Fig. F1).

Appendix H. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2020.103839.

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