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Received: 13 March 2022 | Accepted: 28 September 2022

DOI: 10.1002/pan3.10413

PEOPLE AND NATURE
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Adaptive strategy biases in engineered ecosystems: Implications for plant community dynamics and the provisioning of ecosystem services to people

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Funding information
National Science Foundation, Grant/Award Number: 2021015

Handling Editor: Cecily Maller

Abstract

1. Plant communities in green stormwater infrastructure (GSI) such as biofilters play an integral role in ecosystem services provisioning, such that many design manuals now feature plant lists that guide vegetation selection.
2. This study looks at the implications of those lists for biofilter plant communities and their services, focusing on (1) how plants are selected across US climate zones, (2) whether selected plants exhibit adaptive strategy biases (i.e. towards competitive, stress tolerant or ruderal strategies that might impact ecosystem services provisioning) and (3) whether human-induced selection or natural climatic processes underly any biases revealed.
3. Our results suggest that biofilter plant strategies are significantly biased towards stress tolerance or competitiveness (depending on the climate zone) and away from ruderalness relative to the broader pool of native and wetland-adapted native species.
4. Competitive bias was evident in humid-continental climates and stress-tolerant bias in hot coastal/arid climates, with some degree of anti-ruderal bias present across all zones.
5. These biases are correlated with human concerns related to water availability and climate (water conservation; $p < 0.05$, irrigation; $p < 0.1$, climate extremes; $p < 0.1$). They do not appear to reflect strict climatological limits (i.e. limits that are independent of preferences or design constraints imposed by people) because they are not also evident for native plants.
6. The benefits and costs of relaxing these biases are discussed, focusing on the implications for water quality, hydrologic, and cultural services provisioning and the dynamicity of GSI ecosystems, particularly their capacity to self-repair, a prerequisite for the development of self-sustaining GSI.

KEYWORDS
adaptive strategy, biofilter, CSR type, ecosystem services, green stormwater infrastructure, nature-based systems

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1 | INTRODUCTION

Green stormwater infrastructure (GSI) such as vegetated swales, rain gardens and constructed wetlands, are engineered ecosystems, sometimes referred to as nature-based systems (Moosavi et al., 2021), that are designed to mimic nature and perform target functions (often stormwater capture/infiltration for flood mitigation or pollutant removal) using natural processes (Askarizadeh et al., 2015; NRC, 2009; Walsh et al., 2016). Of the ecological components of GSI, plants are perhaps the best studied. Indeed, efforts to characterize the survival of different plant species in GSI as well as their relative capacity to perform desirable functions (Lundholm et al., 2010, 2015; Payne et al., 2014, 2018; Read et al., 2008; Rippy et al., 2021; Winfrey et al., 2020) have led to a proliferation of plant lists in design manuals used by practicing engineers and landscape architects that are beginning to include information about plant-specific tolerances of common GSI stressors (e.g. transient inundation, deicers; LID SC, 2014; Michigan LID, 2008; NC DEQ, 2018; PA BMP, 2006) and their capacity to provide ecosystem services (e.g. assimilate nitrogen, attract pollinators, etc.; Alabama LID, 2016; NC DEQ, 2018; PA BMP, 2006).

The intent of such lists is laudable; to streamline the establishment of engineered ecosystems with desirable traits, but they may also have downsides. For instance, they can encourage a relatively static view of vegetation communities, whereby initial plant selections are expected to persist, providing stable functional profiles (Dunnett, 2015). In practice, plant communities are dynamic, continuously reconstituting themselves in response to environmental and human factors (e.g. stress and disturbance) in ways that reflect their principal adaptive strategy (i.e. their approach to investing resources to achieve fitness in a given environment) (Grime, 1977; Guo et al., 2018; Pierce et al., 2017; Reich, 2014; Rosado & de Mattos, 2017; Westoby, 1998). Without planning for this dynamicity, we risk (1) generating GSI that gradually lose desired functions over time, (2) heavily investing resources in efforts to combat natural ecological succession and preserve function (effectively swimming against the tide) and (3) preventing designed ecosystems from becoming novel ones with the capacity to self-sustain, a desirable characteristic for any engineered ecosystem (Dunnett, 2015). All of this makes understanding how plants are selected in GSI, and whether that process biases plant communities towards or away from particular adaptive strategies, important for anticipating how plant lists might influence GSI performance in unintended ways. Indeed, one might couch the central premise of this paper as a call for nonlinear causal thinking (Di Baldassarre et al., 2019; Mirchi et al., 2012), the goal being to elucidate unintended consequences of present plant selection practices (e.g. biases in plant adaptive strategy fueled by our own attempts to improve function) and discuss their potential significance.

Recent work by Radhakrishnan et al. (2019) and others (Houdeshel & Pomeroy, 2012; Hunt et al., 2015; Payne et al., 2015; Yuan & Dunnett, 2018) point to at least four types of common plant selection criteria in GSI; (1) design appropriateness (i.e. the capacity to survive engineering design specifications and stressors), (2) climate appropriateness (survivorship of precipitation and temperature extremes), (3) nativeness and (4) enhancement of GSI benefits or co-benefits such as nutrient assimilation, aesthetics and biodiversity. Systematic evaluation of these selection criteria across design manuals, however, is lacking, and their relative importance and variability by climatic region is unknown. This information is important because different selection criteria may result in different adaptive strategy biases, each with distinct implications for plant community dynamics and ecosystem services provisioning that warrant consideration by landscape planners and ecological engineers.

In total, there are 19 possible plant adaptive strategies recognized by CSR theory, anchored by three principal endmembers (Competitive: fast growing, large biomass; Stress tolerant: hardy, resource conservative; and Ruderal: high reproduction by seed, resource acquisitive) (Grime, 1977; Grime & Pierce, 2012; Hodgson et al., 1999). Each strategy represents a characteristic response to stress and disturbance (Grime, 1977) and may, therefore, be indicative of plant dynamics and performance in GSI that experience a particular stress/disturbance profile. In this framework, stress refers to environmental constraints that hinder plant physiological processes or induce metabolic injury, and disturbance refers to damage to extant plant biomass (Dunnett, 2015; Grime & Pierce, 2012). If a system exhibits both extremes (i.e. stress and disturbance) plant survivorship is not tenable; all other possible stress/disturbance pairings have an associated adaptive strategy (Grime, 1977; Grime & Pierce, 2012; Hodgson et al., 1999). Indeed, one can think of the stress/disturbance continuum of CSR as a first order ecological filter that regulates plant species composition (i.e. excluding plant functional types with unsuitable adaptive strategies or, in systems where the range of viable strategies is broad, moderating their relative dominance; Grime & Pierce, 2012; Pierce et al., 2007). Secondary filters that act on integrative combinations of traits impacting local (system-specific) performance further winnow the viable pool, determining the ultimate composition of a plant community (Grime & Pierce, 2012; Rosado & de Mattos, 2017).

In engineered ecosystems where initial plant selections are not necessarily informed by adaptive strategy, more 'filtering' may need to occur. The nature of that filtering will likely depend both on the initial plant species selected and the type/magnitude of stress and disturbance experienced in local GSI. Common GSI stressors may include resource limitation (nutrients or water), transient inundation and metabolic injury from road salt or temperature extremes, among others (Farrell et al., 2013; Parker et al., 2021; Szota et al., 2015; Tu et al., 2020; Yuan & Dunnett, 2018), whereas common forms of disturbance may include erosive flows, wind scour, trampling and biomass loss due to grazing or maintenance activities such as pruning (Beryani et al., 2021; Dellinger et al., 2021; Herzog et al., 2021; Mazer et al., 2001). Accordingly, stress/disturbance profiles (and associated plant adaptive strategies) can be expected to vary in GSI, reflecting differences in initial plant

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selection, local/regional land use, climate regime and GSI type, as well as other factors.

At present, however, only a handful of studies have addressed this issue, primarily on green roofs. The stress/disturbance profile of this GSI form tends to favour ruderal and or stress tolerant plant species over competitive ones, which has prompted dramatic shifts in plant community composition over time in some roof systems (Catalano et al., 2016; Dunnett, 2015; Köhler, 2006; Lundholm et al., 2014; Thuring & Dunnett, 2019). Plant adaptive strategy profiles in other GSI are less well studied, although succession, changes in biodiversity and changes in functional diversity are at times addressed (see Muerdter et al., 2016; Winfrey et al., 2018). This knowledge gap includes rain gardens, bioretention and bioswales (hereafter collectively called biofilters), which have become one of the most common GSI practices for managing urban stormwater; see McPhillips and Matsler (2018) for timelines that illustrate the increasing prevalence of bioswales and micro-biofiltration relative to other GSI forms in recent years. In light of this knowledge gap, our study focuses principally on biofilter plants, their adaptive strategies and the implications of those strategies for within-system dynamics.

Our work employs a recently developed series of globally calibrated equations (Pierce et al., 2017) that use three leaf economic traits (leaf area, leaf dry matter content: the ratio of leaf dry weight to leaf fresh weight and specific leaf area: the ratio of leaf area to leaf fresh weight) to classify the adaptive strategy of biofilter plants. This three-trait framework simplifies the plant classification process (Li & Shipley, 2017; Rosado & de Mattos, 2017; Rosenfield et al., 2019) and makes assessing the range of plants included in biofilter plant lists nationally, tractable. Our study is organized around three principal questions inspired by the knowledge gaps identified above: (1) How are plants being selected for inclusion in biofilter vegetation lists in different climate zones across the continental US?, (2) What is the principal adaptive strategy of biofilter plants in these climate zones and how does it compare to the strategy of native plants in each zone (i.e. do systematic biases in plant adaptive strategy exist)? and (3) If biofilter plant strategies are biased relative to those of native species, what human-induced plant selection processes underly those biases? We explore the implications of our findings for the provisioning of ecosystem services by biofilters to people as well as for plant community dynamics, touching on the value of planning for dynamicity as part of initial GSI design.

2 | METHODS

2.1 | Plant selection practices in current design manuals

2.1.1 | Design manual selection

GSI manuals that included plant lists or provided links to external plant lists were compiled for major climate zones of the coterminous US. Manuals were sourced from state Departments of Environmental Quality or Environmental Protection as well as county or city websites. Geographically dominant Koppen-Geiger climate zones were identified for each manual (ArcGIS pro 2.5.2) and used to sort manuals by climate (Beck et al., 2018)

Biofilter design manuals with recommended plant lists were available for 8 of the 11 major Koppen-Geiger zones, including hot desert (Bwh), cold semi-arid (Bsk), hot-summer Mediterranean (Csa), warm-summer Mediterranean (Csb), humid subtropical (Cfa), Mediterranean influenced warm-summer humid continental (Dsb), hot-summer humid continental (Dfa) and warm-summer humid continental (Dfb) (geographic ranges in Figure 1a).

At least 2 biofilter plant lists were identified per climate zone, with more being compiled in zones with higher spatial coverage (2–3 lists per climate zone spanning 1.5%–3% of continental US land area and 4–6 lists per climate zone spanning >3% of continental US land area) (Table S1). Our intent was to conduct a representative sampling of existing biofilter design manuals, not an exhaustive one. Given this some climate zones will feature more design manuals than evaluated here, particularly zones where GSI installation by the homeowner is incentivized; homeowner design manuals and education/outreach materials were not included in our analysis. University sponsored design manuals with no profile on state/county websites were also not considered, as they may not reflect general practice. A complete list of the design manuals evaluated in this study (28 total) is provided in Table S1.

Because design manuals can be shared and repurposed by different agencies (violating statistical independence assumptions important for Section 2.1.3), the number of manuals referencing a current or former version of another manual was tracked and has been reported in Figure 1b. 13 of the 28 manuals did not reference (and were not referenced by) any other manual, 7 were associated with 1 other manual, 5 with 2 other manuals, 2 with 3 other manuals and 1 (Dfb4, Figure 1b) with 5 other manuals. The resultant number of between-manual associations was relatively small (n = 14), approximately 3.7% of the maximum possible pairwise associations. The most highly referenced manuals were older and from the Northeast or Midwest (i.e. closer to where biofilters were first conceived and adopted; Northeast/Midwest > Southeast/Pacific Northwest > Southwest; Figure 1b) (Roy-Poirier et al., 2010).

2.1.2 | Content analysis

Each design manual was pre-screened to identify code-able document sections featuring plant lists or design details for terrestrial GSI (i.e. sections describing biofilters, bioretention cells, rain gardens, bioswales and/or vegetated swales). See Table S1 for a list of the specific document sections selected for each design manual. Each section was coded using an iterative process, beginning with an initial code key (italicized text, Table 1) containing plant selection categories informed by Radhakrishnan et al. (2019). Coding

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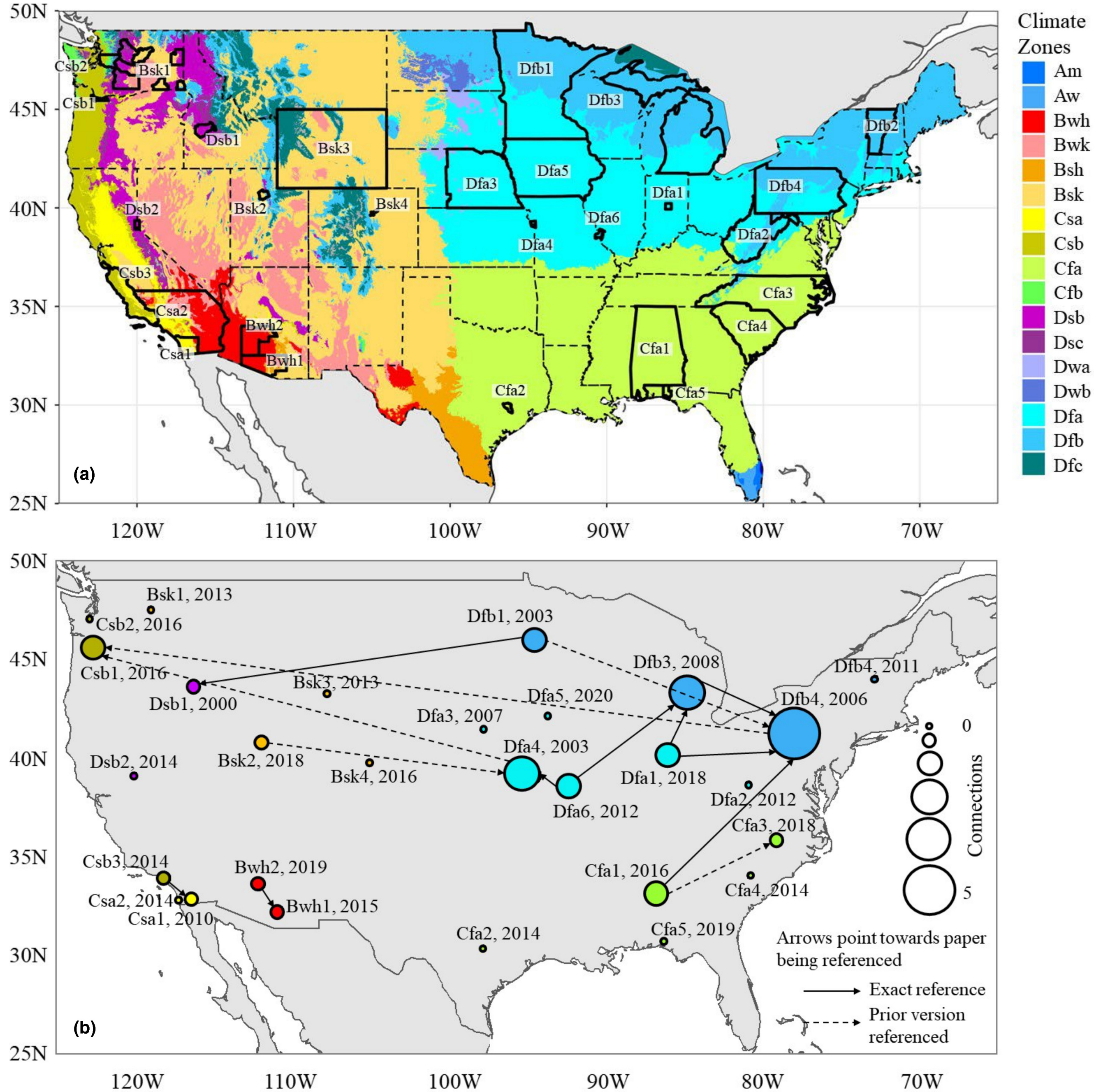

FIGURE 1 (a) Climate zones of the continental United States. Locations where design manuals were sourced are indicated with solid black boundaries and design manual codes (climate zone + manual number; code key in Table S1). The eight climate zones represented in this study include: Hot desert (Bwh: red), cold semi-arid (Bsk: light orange), hot-summer Mediterranean (Csa: yellow), warm-summer Mediterranean (Csb: olive), humid subtropical (Cfa: light green), Mediterranean influenced warm-summer humid continental (Dsb: magenta), hot-summer humid continental (Dfa: cyan) and warm-summer humid continental (Dfb: sky blue). (b) The number of design manuals that reference a current (solid arrow) or prior (dashed arrow) version of another manual. Circle size indicates the number of manuals a given manual references or is referenced by. Design manual codes are the same as in (a) and have been presented alongside the year each manual was written.

was conducted by a single researcher, with eight randomly selected manuals coded in duplicate by a second individual to assess reliability (i.e. consistent interpretation of codes and application to document text) (Elo et al., 2014; Schreier, 2012). Two reliability indices were used, Cohen's kappa (R package, PSYCH) and percent researcher agreement. A kappa score of 0.61 indicating substantial agreement (McHugh, 2012) was required to proceed from the initial to the final stage of coding.

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TABLE 1 Plant selection criteria

Form.Traits: Selection based on growth form (shrub, tree, graminoid, forb) or morphological traits such as height, crown spread, woody versus herbaceous, prostrate versus upright, root form or rooting depth.
Moisture: *Selection based on tolerance of filter media moisture gradients or transient inundation.*
Native: *Selection based on nativeness. May reflect perceptions of native plant survival or intrinsic value.*
Local.Climate: *Selection based on local climate. Includes general references to climate, specific mention of precipitation or temperature extremes, plant drought tolerance or plant hardiness zones.*
Ecoregion: *Selected based on geographic ecoregion or biome. Presumes ecoregion-appropriate plants survive better.*
Irrigation: Selection based on supplemental irrigation needs.
Aesthetics: *Selection based on attractiveness to people (colour, flowers, rustic or manicured aesthetic, cues to care)*
Invasive: Selection based on the desire to avoid invasive or nuisance plant species, including weeds
Maintenance: Selection based on maintenance requirements, including pruning, mowing, weeding, litter & messy fruit.
Soil: *Selection based on tolerance of media/soil, including sandy, low nutrient, low oxygen, & acidic or alkaline soil.*
Life History: Selection is based on plant life history, including references to annual versus perennial, generalist versus specialist, dominance and lifespan (C, S or R strategies would count, but were never specifically mentioned).
Aspect: Selection based on the amount of sun or shade present (solar exposure) at the site.
Exotic: Section of exotic (non-native, but not invasive) plants is permissible. Plant lists may include exotic species.
Salt.Tolerant: *Selection based on ability to tolerate roadway deicers.*
Season: Selection based on seasonal considerations (year-round flowers or colour, mixing deciduous & evergreen).
Biodiversity: *Selection to establish biodiverse plantings (variety of growth forms, species or functional types).*
Wildlife.Value: *Plants selected to attract desirable fauna and provide habitat or food/forage. Includes fauna for observation (birdwatching) lifespan (C, S or R strategies would count, but were never specifically mentioned).*
Safety: Selection to reduce harm (plants that pose a fire risk, have sharp edges or thorns, or are poisonous to humans).
Erosion: *Selection to control flow velocity or winds, preventing soil erosion within the biofilter or downstream.*
Adj.Land.Use: Selection based on adjacent land use (i.e. appropriate for residential neighbourhoods). Expected human interaction based on surrounding land use is a consideration.
Pollutant.Removal: *Plants selected to treat, assimilate and degrade stormwater pollutants.*
Avail.Cost: Selection based on commercial availability (presence at local nurseries when the system is planted) or cost.
DiseaseFauna.Resist: Selection based on resistance to common diseases or grazing by local herbivores.
Infrastructure: Plants selected for characteristics that will not damage green infrastructure (liners, underdrains) or adjacent infrastructure (telephone lines, sidewalks, sub-basements)
Shade: *Selection for shade or urban cooling (shade trees, canopy cover, evapotranspirative or vegetative cooling).*
Regulate.Flow: Selection based on ability to regulate flow velocity (i.e. slow flows).
Tolerate.FlowVel: Selection based on ability to withstand high velocity flows.
Adj.Landscape: Plants selected to maintain continuity with surrounding urban vegetation so that the plant 'fits' the landscape immediately adjacent to the site. Adjacent lands may be native or exotic.
Establishment: Selection based on ease of establishment. Prefer plants that are easy to naturalize and grow quickly.
Infiltration: *Plants selected to maintain infiltration or hydraulic conductivity.*
Tolerate.Pollutants: Selection based on tolerance of stormwater pollutants expected under year-round operation. Excludes salt, which is seasonally applied and cold-climate specific.
Conserve.water: Selection of low water use plants to conserve potable water. The end goal must be resource conservation, not survivorship during periods of low water availability.
Urban: Selection based on tolerance of urban stressors that could impact any urban landscape plant. Include air pollution, increased temperatures from the urban heat island or from light reflection off buildings and tolerance of compacted soils.
Nature screen: Plants selected to screen people from urban landscape features/hazards (visual, auditory, wind screening)
Boundary.Barrier: Plants are selected to define biofilter boundaries, providing a sense of order or purposefullness (cues to care) or a defensive barrier that prevents people from entering the system.
Wind: Selection based on wind present at a site and expected plant wind tolerance given root structure and growth form.
Fragrance: Selection based on olfactory attributes (i.e. pleasant smell of flowers or herbs)
Food.Med.Goods: Plant selection considers human uses including food, traditional medicine and goods (baskets, lumber). Uses may not be recommended, but information about them is provided.
Succession: Plants selected with the understanding that initial choices may be supplemented with volunteer species.
Air.Quality: Selection to improve local air quality. Inclusive of carbon sequestration.

In both of these stages, document sections for each design manual were read in their entirety and any paragraphs pertaining to plant selection were highlighted and coded. Paragraphs were assigned more than one code category if they addressed multiple plant selection topics and paragraphs that could not be coded using the initial key were assigned temporary (de-novo) code categories. Each de-novo category was discussed and collaboratively refined until consensus was reached and a final code key was generated (see plain text additions in Table 1). All document sections were revisited using this final key, again with 8 randomly selected manuals evaluated in duplicate. Final coding assignments were considered reliable if percent researcher agreement exceeded 0.8 and a kappa score of 0.61 was met (McHugh, 2012).

2.1.3 | Correspondence analysis

Dominant patterns in plant selection criteria (i.e., from Table 1) across climate zones were identified using correspondence analysis (CA; R package, FactoMineR, Lê et al., 2008). Data were input as percentages (i.e. percent use of each code concept in each design manual). CA modes were only interpreted if they were significant at a $p < 0.01$ level using resampling-based approaches, hereafter referred to as dominant CA modes (Rippy et al., 2017). Plant selection criteria that contributed significantly to dominant modes (i.e. that characterize the patterns those modes represent) were identified using nonparametric bootstrapping (R package, CABOOTCRS).

CA was performed on both the entire plant selection criteria dataset and on a reduced dataset with the most frequently referenced design manual removed (Dfb4, Figure 1b), reducing the total number of connections between design manuals by ~1/3. This was used as a statistical check to determine whether between-manual connectivity (a form of statistical dependence) significantly influenced our CA.

2.2 | Adaptive strategy biasing

The adaptive strategy profile of plants recommended for use in biofilters was estimated (details in Section 2.2.1) and compared to (1) native plants (i.e. plants native to the same climate zone each biofilter manual was intended for) and (2) wetland-adapted native plants, allowing us to determine whether biofilter plant species exhibit adaptive strategy bias. The second of these comparisons (i.e. with wetland-adapted natives) was performed because species found in wetlands tend to be tolerant of immersion and may therefore be a good benchmark for comparison with biofilter plants.

Climate-adapted native species were drawn from Pierce et al.'s (2017) global analysis of plant adaptive strategy, which included 677 species native to North America within one or more of the eight climate zones of interest (Figure 1). Native plant ranges were determined using bplant.org (https://bplant.org/search.php), the GRIN taxonomy for plants (https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch) and the USDA plants database (https://plants.sc.egov.usda.gov/java/). Climate zones and native ranges were georeferenced (ArcGIS Pro 2.5.2) to determine which species were native to each zone. Of the climate-adapted natives evaluated, 58% have been observed in wetlands (i.e. are classified as FACU: *up to 33% occurrence*, FAC: *34%–66% occurrence*, FACW: *67%–99% occurrence*, or OBL: *>99% occurrence in wetlands*, in accordance with the National Wetland Plant List; Lichvar, 2012). A subset of these natives are also biofilter species, recommended for use in at least one design manual (i.e. 27% of native plants and 32% of native wetland plants).

2.2.1 | Adaptive strategy classification

Two approaches were used to determine the adaptive strategy of each plant species. Approach one involved direct estimation using Pierce et al.'s (2017) globally calibrated equations. Species-specific leaf traits (leaf dry matter content, specific leaf area and leaf area) required as inputs were compiled from the literature or experimentally determined by the authors. Experimental measurements were made in accordance with standard methods (Cornelissen et al., 2003), with leaf area estimates including the petiole (Pierce et al., 2017). In approach two, adaptive strategy classifications were compiled from the literature. For analytical consistency, only estimates made using Pierce et al.'s (2017) approach (StrateFy) were used. This includes the Pierce et al. (2017) publication itself, which reported adaptive strategies for all plants in the TRY database where leaf trait information was available. Evaluation of TRY records post-2017 did not yield additional trait information (i.e. complete sets of all three leaf traits that could be used to classify more biofilter species. Table S2 lists the adaptive strategy of all biofilter plants classified in this study. Table S3 does the same for climate-adapted natives, noting which species are both climate-adapted and present in wetlands.

2.2.2 | Significance testing

To determine if the adaptive strategy profile of biofilter plants differed significantly from native or native-wetland plants, a nonparametric bootstrap comparison of geometric medians was performed. The geometric median was used because it is a robust indicator of central positioning in data with multiple dimensions (Weiszfeld & Plastria, 2009) and adaptive strategy classifications are effectively three dimensional (C, S and R). 10,000 bootstrapped realizations of the geometric median were estimated for (1) biofilter plants, (2) native plants in each climate zone and (3) wetland-adapted native plants in each climate zone, forming point clouds in ternary space that illustrate the range of possible medians for each plant group (R package, PRACMA). Point clouds were compared to determine if adaptive strategy biases were present (e.g. between biofilter plants and native or native-wetland species), and, if so, along which principal dimensions (C, S or R). Point clouds that did not overlap were considered significantly different, as no portion of their possibility space was shared. This constitutes a more stringent statistical threshold than the typical 95% confidence.

2.3 | Drivers of adaptive strategy bias

Combined fourth-corner and RLQ analysis was used to evaluate the role of plant selection practices and local meteorology in establishing adaptive strategy biases across climate zones (Dray et al., 2014). RLQ is a form of co-inertia analysis, whereby drivers of plant selection in each climate zone (anthropogenic or natural) can be linked to species-specific functional types such as adaptive strategy through the presence or absence of species possessing those strategies in each zone (Dray et al., 2014). The approach involves three matrices, R, L and Q. In our analysis, L, the community matrix, indicates which plant species are included in biofilter design manuals in each climate

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zone. It has binary values as entries (1 if a plant is recommended for use in a given zone and 0 if it is not). Q, the functional trait matrix, links plant species to their respective adaptive strategies, and R, the environmental matrix, reports averages for plant selection criteria and meteorological characteristics by climate zone. Our environmental matrix included the following variables: (1) all significant CA modes (i.e. dominant patterns in plant selection criteria) identified in Section 2.1.3, (2) frequency of occurrence scores for any variables contributing significantly to those modes at a $p < 0.01$ level and (3) annual and seasonal meteorological characteristics (annual mean temperature, mean annual rainfall, the standard deviation of mean monthly temperature: seasonal temperature and the coefficient of variation of mean monthly rainfall: seasonal rainfall). Meteorological characteristics were estimated using a set of multi-band rasters from the WORLDCLIM dataset (Hijmans et al., 2005). Rasters were spatially joined with our georeferenced Koppen Geiger climate zones (Beck et al., 2018) to estimate zone-specific averages for all meteorological variables (ArcGIS Pro 2.5.2).

RLQ analysis was conducted using R package ADE4 (Dray & Dufour, 2007). Global significance of this analysis (i.e. the presence of an overarching relationship between adaptive strategy and plant selection criteria or meteorological variables) was assessed using the S_{RLQ} statistic (Dray et al., 2014; Dray & Legendre, 2008). Fourth-corner analysis was used to evaluate bivariate associations between specific adaptive strategies and meteorological or plant selection variables (Dray et al., 2014). Significance was assessed using Monte Carlo approaches (50,000 permutations) as in Dray et al. (2014) ($p < 0.05$ level, corrected for multiple comparisons via the false discovery rate method; Benjamini & Hochberg, 1995).

For comparison purposes, and to facilitate identification of natural climatic effects on plant adaptive strategy across climate zones (i.e. absent the human manipulation that characterizes biofilter species), the RLQ analysis described above was repeated using (1) all plants in our climate-adapted native species pool and (2) only the subset present in wetlands, rather than plants recommended for use in biofilters. For these analyses, the environmental matrix included only meteorological variables (plant selection criteria were omitted), and the community matrix indicated which species were native to which climate zones rather than which species were recommended for use in biofilters by climate zone.

3 | RESULTS

3.1 | Plant selection criteria

Inter-researcher reliability was high across design manuals evaluated in duplicate, indicating that coded plant selection concepts were consistently interpreted and applied. Percent agreement across researchers was 71% for the initial key and 83% for the final key, the latter exceeding our target threshold of 80%. Cohen's kappa was 0.63 and 0.76 for initial and final code keys, respectively, also indicative of substantial agreement (McHugh, 2012).

Of the 40 plant selection concepts evaluated, twelve were referenced more often than expected due to chance (i.e. more than 2.5% of the time, on average, across all design manuals; Figure 2). These criteria, in order of decreasing mention, include selection based on (1) growth form or morphological traits, (2) tolerance of soil moisture and transient inundation, (3) nativeness, (4) local climate appropriateness, (5) ecoregion, (6) irrigation requirements, (7) aesthetics, (8) lack of invasiveness, (9) maintenance considerations, (10) tolerance of biofilter media, (11) life-history characteristics and (12) sun/shade requirements. Criteria pertaining to water quality and volume regulation (pollutant removal, flow regulation, infiltration) were only infrequently mentioned (ranked 21, 26 and 30 out of 40; Figure 2). A detailed description of each selection criteria is provided in Table 1.

CA revealed two significant CA modes ($p < 0.01$ level) that explained 27% of the variance in plant selection practices (Figure 3). No other modes were statistically significant. CA Mode 1 distinguishes design manuals (small circles, Figure 3) where plants were significantly more likely to be selected based on local climate, irrigation needs and water conservation principles (negative CA1) from

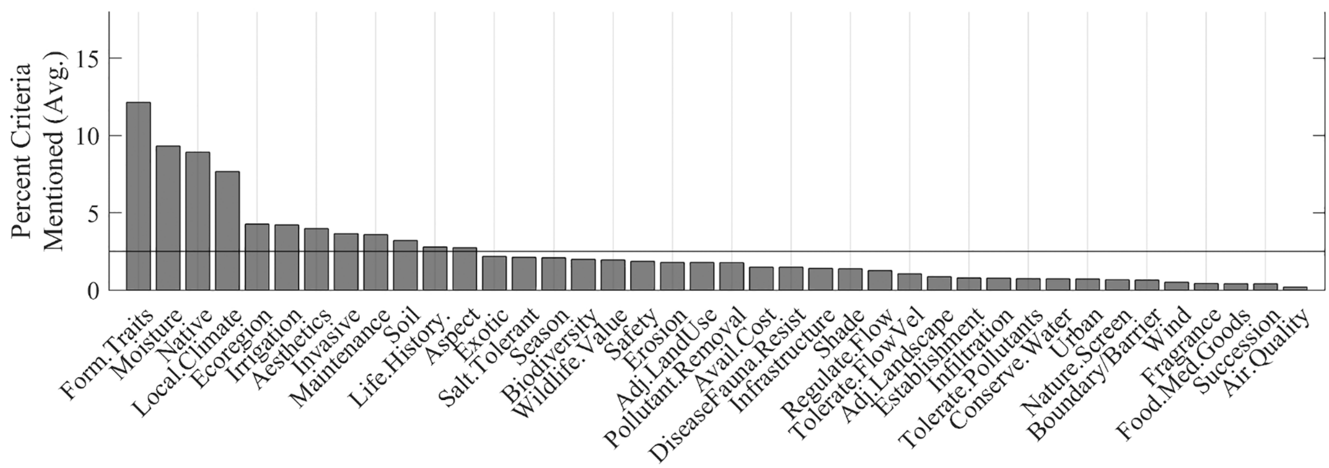

FIGURE 2 Percent of the time each plant selection criteria is mentioned on average across all design manuals. The solid black line marks the %time each criterion would be mentioned due to chance (i.e. 1 in 40 or 2.5%). See Table 1 for individual criteria definitions.

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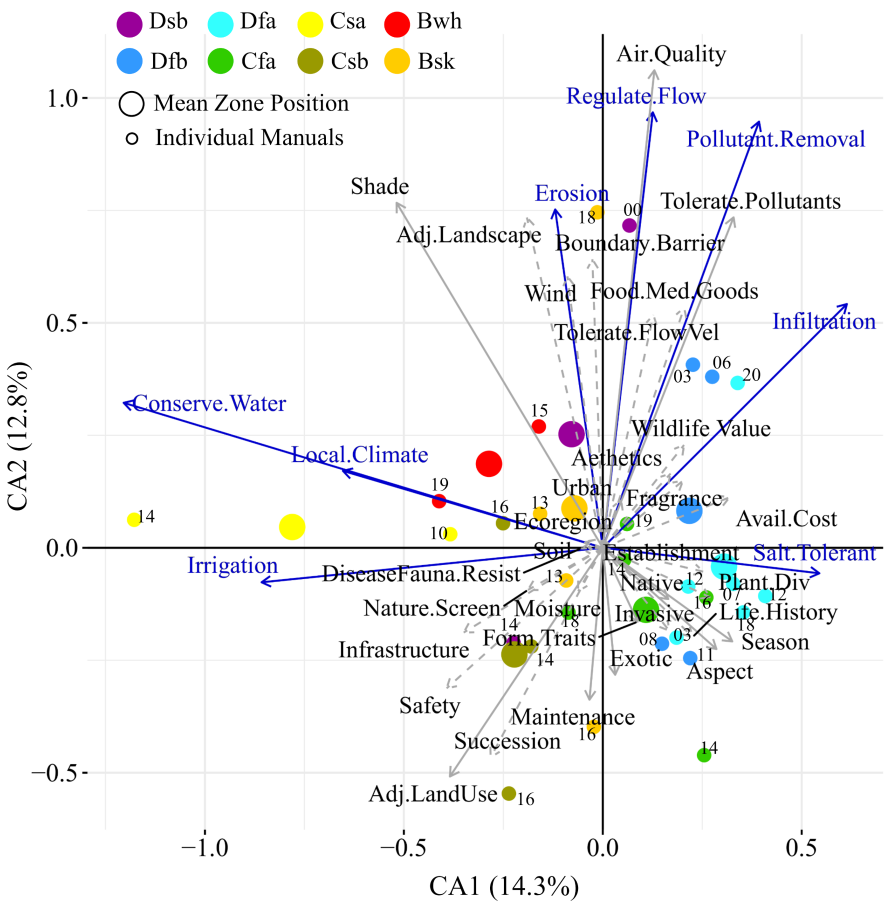

FIGURE 3 Correspondence analysis (CA) biplot of plant selection criteria by design manual (small coloured circles). Manuals belonging to the same climate zone are shown in corresponding colour (same as Figure 1), and their mean position in CA-space is indicated using a large circle of corresponding colour. The x-axis shows the dominant pattern in plant selection practices (CA mode 1). A significant, secondary pattern (CA mode 2) is shown on the y-axis. All plant selection criteria that contributed significantly to CA mode 1 or 2 at a $p<0.01$ level ($p<0.05$ level) are indicated using solid blue (grey) vectors; the direction of strike indicates the mode they contribute principally to. Criteria that do not contribute significantly to either mode are shown using dashed grey vectors. Criteria names are abbreviated as in Figure 2. Numbers refer to the last two digits of each manuals publication year (e.g. 18 for 2018).

manuals where plants were more likely to be selected based on salt tolerance and their capacity to facilitate stormwater infiltration (positive CA1; blue arrows with a horizontal strike are significant with respect to CA1, Figure 3). Manuals from climate zones Csa, Bwh, Csb and to a lesser extent Dsb were located in negative CA1 space, whereas manuals from climate zones Cfa, Dfa and Dfb were located in positive CA1 space. The second CA mode distinguishes design manuals where plants were significantly more likely to be selected based on their capacity to provide traditional GSI services such as pollutant removal, flow regulation and erosion reduction (positive CA2) from those where plants were less likely to be selected based on their capacity to provide these services (negative CA2; blue arrows with a vertical strike are significant with respect to CA2, Figure 3). Manuals from climate zones Bwh, Csa and to a lesser extent Dsb, Bsk and Dfb were located in positive CA2 space, whereas manuals from climate zones Csb, Cfa and Dfa were located in negative CA2 space. Additional selection criteria contributed to these modes, but more weakly (solid grey arrows, Figure 3; significant at a $p<0.05$ level). These include seasonal colour (season), plant sun/shade requirements (aspect) and nativeness (positive CA1), shade provisioning, air quality and pollutant tolerance (positive CA2), and allowance for exotics, growth form/traits, maintenance and adjacent land use (negative CA2).

The year a design manual was written does not appear to exert strong influence over its location in CA space beyond the tendency for manuals from western US states/counties (negative CA1 space) to be more recent, written over the past 10 years (2010–2019). Indeed, the oldest manual (Dsb1, 2000) and the most recent manual (Dfa5, 2020) actually lie in the same CA quadrant (positive CA1, positive CA2), illustrating that manuals written years apart can actually be more similar in their plant selection criteria than manuals written in the same year (design manuals from 2014 are present in all but the upper right CA quadrant).

When CA was rerun omitting the most cross-referenced design manual (Dfb4), observed patterns in plant selection criteria did not substantively change (see Figure S1). Two significant modes still captured 27% of the variance and all original variables that significantly contributed to each mode remained significant. This suggests that, although design manuals may inspire one another, the patterns in plant selection practices across design manuals resolved here are unlikely to be driven by this effect.

3.2 | What biofilter plants are recommended?

No plant species were recommended for use in all biofilter design manuals or climate zones. The species recommended most often (16 of 28 manuals; all climate zones except Bwh and Csa) was *Juncus effusus*, an obligate wetland rush. The second most recommended plant (14 of 28 manuals; Bsk, Cfa, Dfa and Dfb)

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was *Panicum virgatum*, a facultative upland bunch grass. Four species were more cosmopolitan than all other species (i.e. recommended for use in more climate zones; 6 of 8). These include the aforementioned *Juncus effusus*, as well as *Bouteloua curtipendula* (grass), *Cornus sericea* (shrub) and *Celtis occidentalis* (tree). In some instances, plant lists within a climate zone were more similar to one another than to lists from other zones (see, for instance, Dfa3 through Dfa6, where plant lists were most similar (36%–51% shared plants) to other lists in zone Dfa; Figure 4). There were also instances, however, where plant lists were actually more similar across climate zones (see, for instance, Dfb3, where all listed plants were shared with a manual from Dfa, and Dsb1 through Dsb2, where more plants (17%–31%) were shared with manuals from climate zones Bsk or Csb than Dsb; Figure 4).

3.3 | Plant adaptive strategies

Across all design manuals, only 32% of plant species recommended for use in biofilters could be classified to an adaptive strategy (min of 9% in Bwh, max of 50% in Dfb), highlighting a knowledge gap in our current trait-based understanding of biofilter plants. A consequence of this, is that we must interpret the adaptive strategies of biofilter plants using a subsample, making it important to consider whether that subsample is representative. Because adaptive strategy is correlated with growth form (Pierce et al., 2017), we elected to evaluate subsample representativeness in each climate zone by comparing the growth form distribution of each subsample to its corresponding distribution in full plant lists (nonparametric bootstrap comparison of proportions; Manly, 2007). This analysis demonstrated that subsamples and full plant lists had statistically comparable growth form distributions in all climate zones (i.e. the average percent forbs, graminoids, shrubs and trees in each climate zone's CSR subsample (circles in Figure 5) fell within the Bonferroni-Holm corrected 95% confidence bounds (Holm, 1979) estimated for corresponding full plant lists (lines in Figure 5)). While this does not preclude bias in our classified subsample, it does indicate that obvious adaptive strategy biases due to over or under-representation of specific growth forms are unlikely. See SI methods for a discussion of differences in the growth from distributions of biofilter plants by climate zone.

3.3.1 | Adaptive strategy bias

The median adaptive strategy of native plants and native wetland plants (our point of comparison for biofilter plants) were not significantly different, although native wetland species tended to be more ruderal (right skewed) than the overall native pool; note overlap of native plant geomedians (large black circles) and native wetland plant geomedians (large white circles) in Figure 6. Neither differed significantly by climate zone as evidenced by the comparable location of both geomedians and their corresponding confidence clouds (small black and grey points, respectively) across climate zones (Figure 6). Median adaptive strategies for native and native wetland plants were 20%–24% C, 40%–49% S and

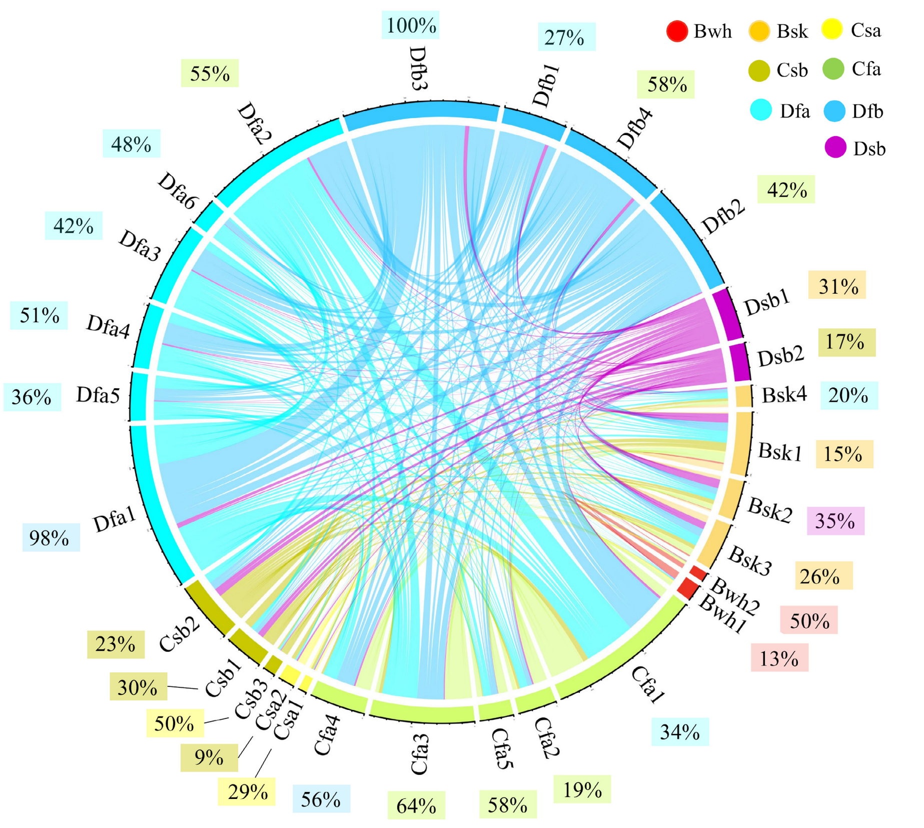

FIGURE 4 Chord diagram indicating how plant species are shared across biofilter design manuals. The size of outer ring segments, which represent design manuals (code key in Table S1), indicate the number of times plants from one manual appear in all other manuals. The width of individual chords indicate the number of plants shared between any pair of manuals. Outer ring colours reflect the climate zone a design manual is from (same colour scheme as Figure 1). Chord colours also reflect climate zone; note that when plants are shared by manuals from two different zones, chord colour will arbitrarily reflect one of the two. Outer ring notation (i.e. colour and percentage values) indicate the maximum percentage of plants each design manual shares with another manual as well as the climate zone that other manual is from.

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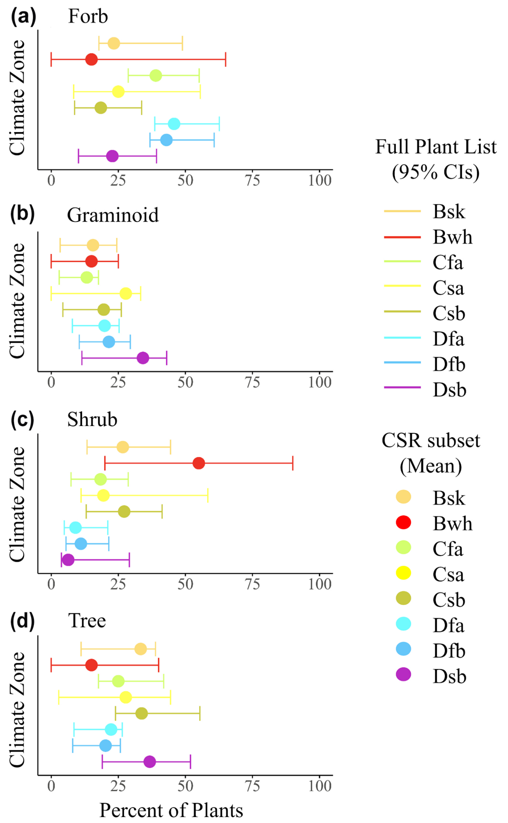

FIGURE 5 Comparison of biofilter plant growth form distributions between full plant lists and the subset of those lists classified to adaptive strategy (CSR subsets) in each climate zone. Climate zones are differentiated by colour (same as Figure 1) and the percent of plants belonging to different growth forms in each zone are shown in different panels: (a) forbs, (b) graminoids, (c) shrubs and (d) trees. Solid lines are 95% confidence bounds about the average percent occurrence of each growth form in full plant lists, and coloured circles illustrate the average percent occurrence of each growth form in CSR subsets. CSR subsets fall within estimated bounds for full plant lists for all growth forms, in all climate zones.

30%–37% R, falling right on the border between S/CSR and SR/CSR classifications. Within each climate zone, the adaptive strategy of individual natives (wetland-adapted or otherwise) was variable, as evidenced by the spread of the mid-sized grey circles in Figure 6, which fill the majority of CSR space.

Unlike climate-adapted natives and native wetland plants, the median strategy of biofilter plants varied significantly by climate zone (note differences in the position of biofilter plant geomedians (large coloured circles) and their corresponding confidence clouds (small coloured points) by zone, Figure 6). The median adaptive strategy of biofilter plants in hot desert and hot summer-Mediterranean climates (Bwh, Csa; Figure 6a,c) was S/CS, the median adaptive strategy of biofilter plants in cold semi-arid, warm-summer Mediterranean and Mediterranean-influenced warm summer humid climates (Bsk, Csb, Dsb; Figure 6b,d,f) was S/CSR, and the median adaptive strategy of biofilter plants in humid subtropical, hot-summer humid and warm summer humid climates (Cfa, Dfa, Dfb; Figure 6e,g,h) was CS/CSR.

Across all climate zones biofilter plants were biased away from ruderal strategies and towards stress-tolerant or competitive ones (note the paucity of mid-sized coloured circles in the lower right corner of each ternary diagram and the left skew of biofilter geomedians relative to native geomedians in all zones; Figure 6). Anti-ruderal bias was significant in Bwh, Bsk, Csa and Csb. It was also significant in Dsb, but only with respect to wetland natives, not native plants in general. The solid black line in each ternary diagram (Figure 6) is intended to help guide significance assessment by marking the least ruderal edge of the confidence clouds for natives; when biofilter confidence clouds lie entirely to the left of this line, it indicates they are significantly less ruderal than either the broader native species pool or native wetland plants.

In Bwh, Csa and Csb, biofilter plants were biased towards stress-tolerant strategies relative to both native plants in general and native wetland species (Figure 6a,c,d). This bias was only significant for Csa, where the biofilter confidence cloud lies to the left of the dotted black line at the most stress tolerant edge of the confidence clouds for native plants (Figure 6c). Biofilter plants in the remaining five zones were biased towards competitive strategies, particularly relative to the general native pool, which was slightly less competitive than wetland-adapted natives (Figure 6b,e–h). This bias was only significant for Dfb, where the biofilter confidence cloud lies entirely above the dashed black line marking the most competitive edge of the confidence clouds for native plants (Figure 6h).

3.4 | RLQ analysis

The S_{RLQ} statistic for biofilter plants was significant ($p = 0.001$), indicating that a relationship between biofilter plant adaptive strategy and plant selection criteria or meteorological variables is present across climate zones (Figure 7a). The same was not true for native plants or native wetland plants ($p = 0.56$ and 0.73, respectively), where adaptive strategy profiles varied little by climate zone (note the weak correlations between adaptive strategy, meteorological variables and the principal RLQ axis (RLQ 1), which captures the primary pattern they share (i.e. shared inertia), Figure 7b,c).

FIGURE 6 Comparison of biofilter, native plant and native wetland plant strategies by climate zone. Medium sized circles indicate individual plant strategies, large circles are geomedians and small circles show statistical confidence about geomedians. Biofilter plants are in colour (same as Figure 1) and native plants are greyscale, ranging from black (natives) to white (wetland natives). The solid black line marks the least ruderal, the dashed black line the most competitive and the dotted black line the most stress tolerant edge of confidence clouds for native plant geomedians (both groups). bio, biofilter; C, competitive; Geomed-all, native geomedian; Geomed-w, native wetland geomedian; nat, native; nat-w, native wetland; R, ruderal; S, stress tolerant

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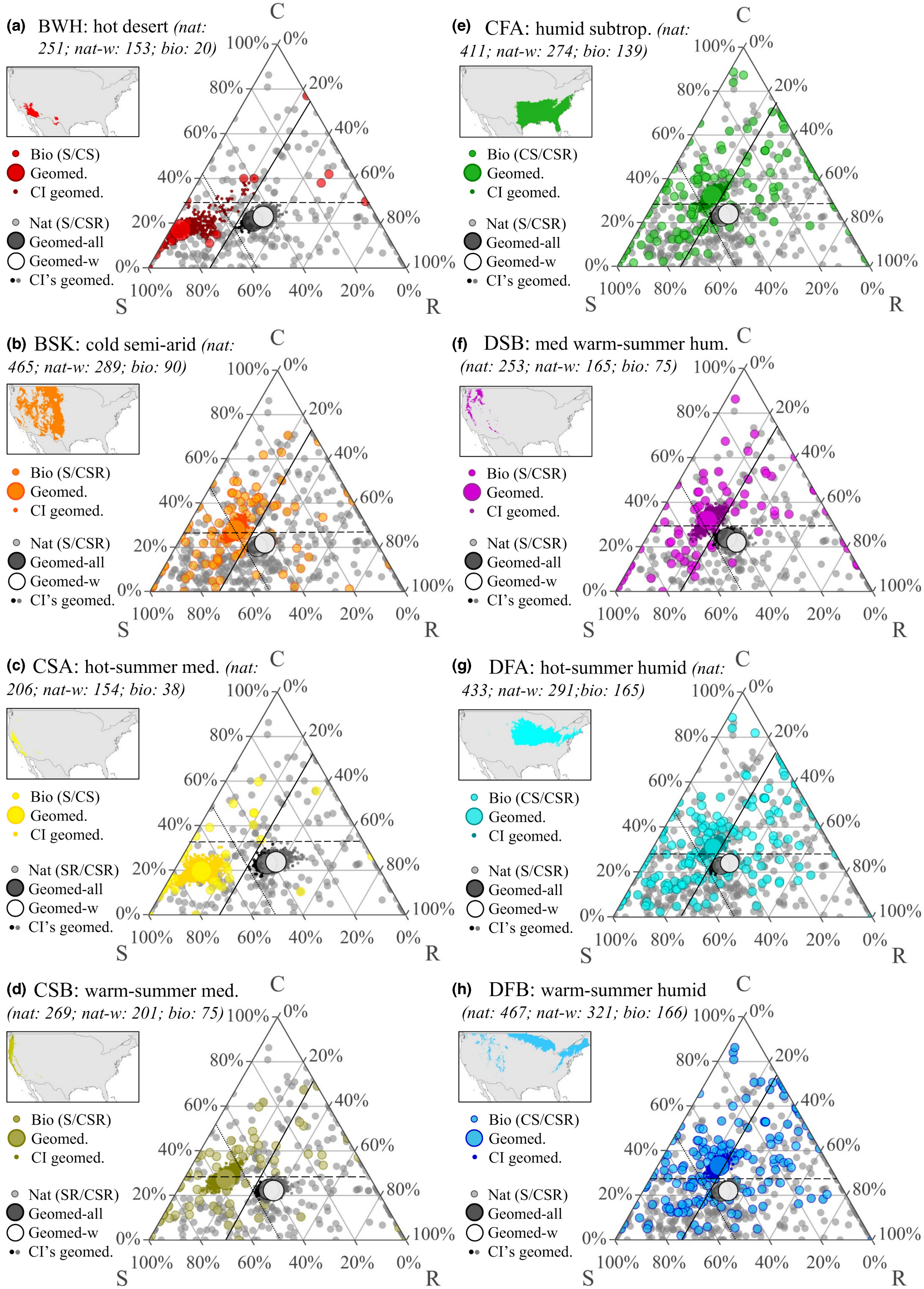

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For biofilter plants, RLQ 1 captured 99% of shared inertia between plant selection criteria, meteorological variables and adaptive strategy. Stress tolerance loaded significantly and positively on this axis, whereas competitiveness and ruderalness loaded significantly and negatively (Figure 7a). The coefficient of variation of mean monthly rainfall (CV.R) was the only meteorological variable significantly associated with RLQ 1, with stress tolerant species featuring more prominently in plant lists from climate zones where rainfall was seasonally variable (Figure 7a).

RLQ 1 was also significantly associated with CA1, the dominant pattern in plant selection criteria across climate zones; positive CA1 loaded with competitive and ruderal strategies and negative CA1 loaded with stress tolerant strategies. Three of the plant selection criteria that contributed significantly to CA1 (Figure 3) were also significantly (or marginally significantly) associated with RLQ 1; Climate zones where plant selection was most influenced by water conservation targets ($p < 0.05$), the desire to reduce supplemental irrigation ($p = 0.06$), or climate-related survivorship concerns ($p = 0.08$) were more likely to favour stress tolerant species in biofilter plant lists (Figure 7a). Selection criteria related to salt tolerance or infiltration were associated with more competitive or ruderal strategies, but not significantly so (Figure 7a). CA2, the second dominant pattern in plant selection criteria across climate zones was not significantly associated with RLQ 1 (Figure 7a). Given this, pairwise associations between individual CA2 criteria and RLQ 1 were not evaluated.

4 | DISCUSSION

Across biofilter design manuals the most frequently mentioned selection criteria were generally consistent with Radhakrishnan et al.'s (2019) work in Singapore, illustrating the broad geographic applicability of concerns related to climate, engineering design constraints (particularly soil type and transient inundation) and co-benefits such as aesthetics. Criteria associated with water quality or volume regulation, however, were infrequently mentioned, highlighting a gap between current plant selection practices and key regulating services (the focus of recent work by Payne et al. (2018)).

The prevalence of selection criteria keyed to engineering design constraints across all manuals and climate zones (Figure 2) serves as an important reminder that biofilters are designed novel ecosystems with unique characteristics (e.g. specialized media with higher sand content than native soils and (consequently) lower water retention, as well as flow rerouting from impervious surfaces, leading to flashy, transient inundation and elevated pollutant loads with no natural analogues) (Hunt et al., 2012; Parker et al., 2021; Tirpak et al., 2021). Indeed, widespread attention to stressors like these across all climate zones may help explain why biofilter plants appear relatively stress tolerant overall (median adaptive strategy of S/CS to CS/CSR, depending on the zone; Figure 6).

Not all plant selection criteria were equally prevalent across climate zones, however (see Figure 3), and differences in these criteria appear to coincide with zone-specific adaptive strategy biases in

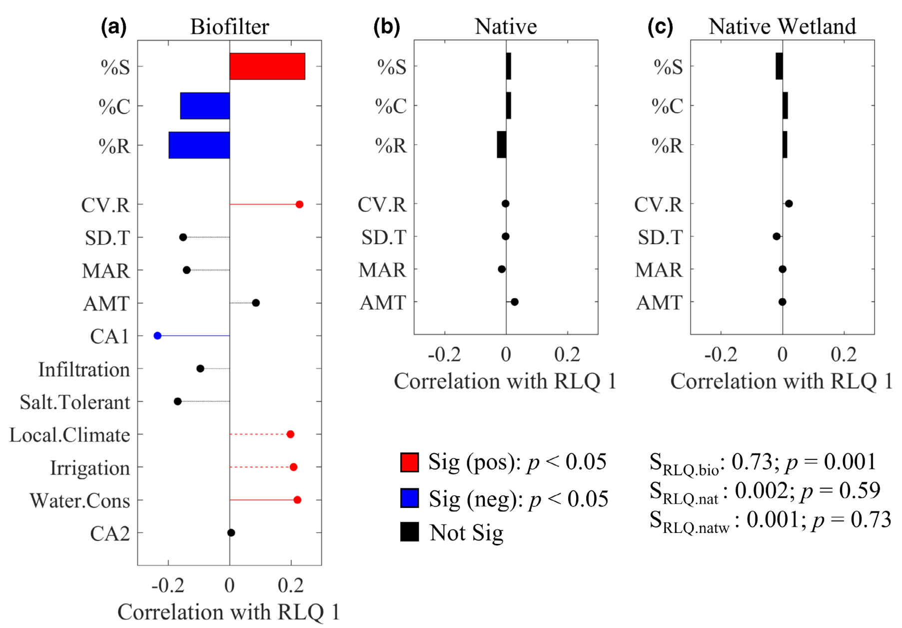

FIGURE 7 Joint RLQ and fourth corner analysis for (a) biofilter plants, (b) native plants and (c) native wetland plants. Variables contributing significantly ($p < 0.05$) and positively to RLQ axis 1 are shown using red boxes (adaptive strategy) or solid red lines (meteorological or plant selection variables). Variables contributing significantly and negatively to RLQ axis 1 are shown using blue boxes (adaptive strategy) or solid blue lines (meteorological or plant selection variables). Relationships that are marginally significant ($p < 0.1$) are shown using dashed lines of corresponding colour. All nonsignificant relationships are shown in black. AMT, annual mean temperature; C, competitive; CA1 and CA2, the first and second correspondence modes from Figure 3; CV.R, coefficient of variation of mean monthly rainfall; MAR, mean annual rainfall; R, Ruderal; S, stress tolerant; SD.T, standard deviation of mean monthly temperature; Water. Cons, water conservation

biofilter plants that are not evident in native plants or native wetland plants (Figure 6). This suggests that the factors driving observed differences in biofilter plant strategies across climate zones may not have natural climatic origins; If they were purely climate driven (i.e. independent of design constraints or human preferences), we'd expect to observe similar patterns across native species, correlated with meteorological variables. In practice, no such relationships were observed (Figure 7b,c). Indeed, the degree of actual invariance in the median strategy of native plants by climate zone was somewhat surprising. However, we recognize that most climate-driven patterns are reported for individual species, plant communities or common ecosystem typologies (e.g. forests) along a climate gradient (Han et al., 2021; Rosenfield et al., 2019; Sartori et al., 2019), not in aggregate (i.e. spanning biomes and growth forms, which themselves exhibit characteristic adaptive strategy profiles (Pierce et al., 2017) that may obscure climate-driven patterns).

In contrast to native plants, the adaptive strategy profile of biofilter plants was significantly correlated with meteorological variables (precipitation seasonality) and key plant selection criteria (local climate, irrigation and water conservation) (Figure 7a), suggesting that adaptive strategy biasing may be driven (at least in part) by local water availability, and concerns about it, in each climate zone. People's desire for vegetation that can survive long dry periods and achieve water conservation targets may select for species that tolerate and survive drought (more likely to be stress-tolerant) rather than species that escape it (more likely to be ruderal; see Volaire, 2018) in climate zones where rainfall is seasonal (Bwh, Csa, Csb; rainfall coefficient of variation: 0.54–0.81), even though both strategies would be present under natural conditions; note the broad range of strategies that native plants possess in each climate zone (Figure 6). Similarly, in zones where plant selection is less constrained by water availability concerns (Cfa, Dfa, Dfb; rainfall coefficient of variation: 0.25–0.38), species with high resource needs (for instance, competitive plants) might be selected more often. This is not to imply that competitiveness is synonymous with water resource availability or that stress tolerance is synonymous with drought tolerance, rather that some of the adaptive strategy biases we see in biofilter plant lists may have arisen as a consequence of the way water resources influence people's plant choices.

Some of this bias may be unavoidable, caused by the additional stress plants face in water scarce climates due to engineering design choices that are core to biofilter function (for instance use of sand, sandy loam or loamy sand filter media, which promotes infiltration, but retains less water to support plant growth during dry times; Tirpak et al., 2021). However, our results suggest that adaptive strategy bias may also be a reflection of how we do business (i.e. our motivations, such as water conservation, or goals for GSI plants, such as persistent above-ground cover), which constrain plant selection in ways that are not strictly necessary from a climatological standpoint. This is not to say that all plant strategies will be equally successful under all conditions. Local site constraints and microclimate clearly need to be considered (Guo et al., 2018; Utah DEQ, 2018). Rather, we aim to draw attention to the possibility that there may be room for a range of plant selection options in biofilters that aren't presently captured in today's plant lists. The remainder of this discussion will consider this possibility, exploring the implications of various adaptive strategy profiles (competitive, stress tolerant and ruderal) for biofilter ecosystems and their services.

4.1 | Implications of competitive strategy biasing

4.1.1 | Nutrient acquisition and pollutant removal

Competitive plants often exhibit higher growth rates and are resource acquisitive, requiring more nutrients to support rapid growth (Grime & Pierce, 2012; Pierce et al., 2017). From an ecosystem services perspective, this means that a competitive strategy bias has the potential to enhance nutrient removal (Payne et al., 2018). Nutrient removal is a relatively common biofilter design objective (although not one plants are frequently selected for; ranked 21 of 40, Figure 2), with nitrate, which exhibits variable fates in GSI from net removal to leaching, being of particular regulatory concern (Kohlsmith et al., 2021; Payne et al., 2014)

Nitrate uptake by competitive plants might help reduce its leaching by biofilters, at least in the short term. The long-term implications of this sink are less clear, given that plants eventually return sequestered nutrients to the soil as litter, and there is evidence to suggest that the more resource acquisitive a plant is, the more biodegradable its tissues will be, particularly its leaves (Freschet et al., 2012). The net effect of rapid assimilation coupled with enhanced degradability on nutrient removal in biofilters is not well understood. It is also only part of the nutrient balance story; Ultimate nutrient balances may be as much a function of plant-microbe associations (e.g. with rhizosphere bacteria (Cardenas et al., 2021; Taylor & Townsend, 2010) and mycorrhizal fungi (Bergmann et al., 2020; Palacios et al., 2021; Winfrey et al., 2017)), maintenance activities undertaken by people (e.g. harvesting plant biomass instead of allowing it to return as litter; Herzog et al., 2021), and abiotic processes (e.g. sorption of nutrients like phosphorous to biofilter soils; Marvin et al., 2020), as plant acquisitiveness or conservativeness in accordance with adaptive strategy.

4.1.2 | Water balance, cooling and aesthetics

In addition to being nutrient acquisitive, competitive plants tend to use more water (Payne et al., 2018; Schrieke & Farrell, 2021), a challenge in regions that are water stressed, but a potential benefit in terms of evaporative cooling and stormwater volume regulation (important in positive CA2 climate zones; Figure 3). Competitive species also have the potential to provide other ecosystem services in GSI. For instance, trees, which have an average adaptive strategy of competitive-stress tolerant (Pierce et al., 2017), provide more shade than any other growth form, a particularly important service in Bwh (Figure 3). Many popular flowering plants also have competitive

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strategies (i.e. blue flag iris, sunflower, peonies) and appreciable aesthetic value (important across all zones, Figure 2). This value has been coined the 'wow factor' by Hoyle et al. (2017), emphasizing the contribution of colourful, flowering plants to perceptions of joy in urban landscapes.

4.1.3 | Survivorship, maintenance-burden and monocultures

Although competitive plants are associated with a variety of services, they do have disadvantages. First, high resource acquisition, while good for pollutant removal and hydrologic services, is not without risk; if the resources needed to support a competitive life strategy become unavailable (for instance during a long-term drought that restricts delivery of runoff and nutrients to the biofilter), competitive plantings may die, necessitating revegetation and increasing the maintenance burden; see Köhler (2006), Catalano et al. (2016), Thuring and Dunnett (2019) and Schrieke and Farrell (2021), for examples of competitive species loss in GSI over time due to resource limitation. Selecting plants to reduce the maintenance burden was a top 10 objective across all climate zones (mentioned more frequently than any service associated with competitiveness, save aesthetics; Figure 2), suggesting that competitive plants may be perceived as riskier than their ecosystem services are worth.

Another disadvantage of competitive plants concerns the potential for competitive dominants to outcompete other species, leading to the formation of monocultures (Buckland & Grime, 2000). Monocultures provide fewer, less diverse, options for habitat, forage and pollination, which could limit the ecological value of biofilters to wildlife (Hostetler & Reed, 2014). Monocultures cannot enhance services through complementarity or facilitation, making them less capable of providing multiple functions and ensuring continuity of function if conditions change (Levin & Mehring, 2015; Loreau et al., 2001). Monocultures can also be less aesthetic than biodiverse plant assemblages (Lindemann-Matthies & Bose, 2008). Such relationships are complex and often contradictory, however, depending as much on the cues to care that signal a planting is intentional as the actual biodiversity of the planting itself (Gobster et al., 2007; Hoyle et al., 2017; Nassauer, 1995; Qiu et al., 2013).

In short, potential disadvantages of competitiveness like those indicated above warrant careful consideration when decisions regarding competitive plant use in GSI are being made.

4.2 | Implications of stress tolerant biasing

4.2.1 | Conservative resource economics and services provisioning

Many, but not all, stress tolerant plants are adapted to survive low resource conditions, with different resource-related stressors (nutrients and water) driving common changes in morphological traits, including those pertinent to CSR-typing such as specific leaf area (Díaz et al., 2004; Fonesca et al., 2001). However, not all traits exhibit common stress responses. Some traits represent adaptations to specific stressors, but not others (e.g. structural modifications to reduce cavitation are an adaptation to drought, but not nutrient stress; Markesteijn et al., 2011), whereas other traits capture stress trade-offs. For instance, in wetland plants, increased specific leaf area can represent both a local stress response, facilitating O_2 and CO_2 exchange when plants are submerged, and be associated with resource-related stress release, placing wetland plants on the acquisitive rather than conservative end of the worldwide leaf economic spectrum (Pan et al., 2020; Wright et al., 2004). This finding is consistent with the slight ruderal or competitive skew exhibited by native wetland plants relative to the general pool of natives in our study (Figure 6). Such examples illustrate how complicated and nuanced linking stress or disturbance to adaptive strategies and eventually ecosystem services can be, underscoring the need to consider any general trends presented here as simplified rules of thumb that need to be verified on a case-by-case basis.

Keeping this in mind, a general rule for stress tolerant plant bias might be that it is the opposite of competitive plant bias from an ecosystem services standpoint. Stress tolerant plants tend to have lower nutrient assimilation and water use, that while beneficial from a water conservation standpoint (important in negative CA1 climates; Csa, Csb, Bwh, Bsk and Dsb; Figures 3 and 7), can limit their capacity to perform important biofilter functions (Payne et al., 2018; Pierce et al., 2017; Rippy et al., 2021). This includes removing stormwater pollutants, regulating flow/volume and providing evaporative cooling (Lundholm, 2015; Lundholm et al., 2010, 2014; Payne et al., 2018).

4.2.2 | Survivorship bias—Stress tolerant plants for resource-poor regions

Although stress tolerance can manifest in different ways, it is safe to say that stress tolerant plants are the survivors of the plant world (Grime & Pierce, 2012; Pierce et al., 2017; Volaire, 2018), a characteristic that may make them desirable to the biofilter design community where plant survivorship is often paramount. This stance is well captured by the City of Portland's stormwater management manual, which sets a mandatory 2-year warranty period for biofilter vegetation with high survivorship standards: '*a survival rate of 90% is required at all times over the 2-year warranty period; plant replacement is required if the rate is less than 90%*' (SWMM, 2016, p. 390). In regions where resource stress or water conservation goals limit the adoption of resource-acquisitive species, such rules may favour a more stress tolerant species profile. Of course, in biofilters where stress/disturbance is low, or where disturbance is high, plants with other adaptive strategies (competitive and ruderal, respectively) might meet this 'survivorship' need (Grime & Pierce, 2012). This illustrates the importance of clarifying where biofilters fall along the stress/

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disturbance continuum, similar to what has been done for green roofs (see Catalano et al., 2016; Dunnett, 2015; Köhler, 2006; Lundholm et al., 2014; Schrieke & Farrell, 2021; Thuring & Dunnett, 2019).

4.2.3 | Stress tolerance in high recruitment systems

Because biofilters are highly connected to other landscapes, receiving runoff from natural and ornamental features as well as impervious surfaces, recruitment by seed is straightforward, and introduction of ruderals that can take advantage of and colonize gaps between stress tolerant plants, is almost a given (Hitchmough & Wagner, 2013; Hunt et al., 2012; Muerdter et al., 2016). If these species are undesired (e.g. weedy nuisances or even invasives), the maintenance actions necessary to exclude them and allow stress tolerant plants time to fill in, can be extensive (Muerdter et al., 2016). Indeed, we might recognize a maintenance trade-off for stress tolerant plants, where the maintenance burden is relatively low in the long-term due to high plant survivorship (see Section 4.2.2), but high in the short-term due to the slow growth rates of stress tolerant plants, reproductive proclivity of ruderals and high connectivity of biofilters with outside seed sources. Such trade-offs are worth considering when making decisions about biofilter plantings, particularly given the tendency of design manuals to set short term standards (e.g. the warrantee noted above) which may unintentionally prioritize short timescales over long ones.

Underpinning the discussion above is the idea that stress tolerant plants are desirable whereas ruderal weeds are not. From an ecological and ecosystem services standpoint, however, this premise is worth questioning (Del Tredici, 2010; Dunnett, 2015; Schrieke & Farrell, 2021). We will address potential benefits and pitfalls of relaxing anti-ruderal bias (the most consistent bias evident across biofilter plant lists in this study; Figure 6), in Section 4.4.

4.3 | Intermediate strategies

4.3.1 | The case of salt-impacted systems

Our results suggest that biofilter plants tend to be biased stress tolerant in regions where water availability shapes plant selection practices (Figure 6a,c,d, Figure 7a), but that plants in regions experiencing other stressors, such as those posed by winter maintenance chemicals, are not (note slight competitive bias in Dfa, Dfb and Cfa; Figure 3). Why might this be? Salt marsh and coastal dune species often feature stress tolerant leaf traits, which makes generalized decoupling between traits associated with salt tolerance and stress tolerance as we have defined it, an unlikely explanation for this observation (De Battisti, 2021; Flowers & Colmer, 2008). However, not all salt tolerant plants are strict stress tolerators. Several common halophytes typically used in wetter green infrastructure systems (e.g. cattail—*Typha latifolia* and bullrush—*Scirpus* sp.; Fishers SW TSM, 2018; MSM Wiki, 2003; NC DEQ, 2018; PA BMP, 2006), are more competitive, or have intermediate adaptive strategies such as competitive-stress tolerant (Pierce et al., 2017) that match up well with the adaptive strategy biases observed in cold/wet climates like Dfa, Dfb and Cfa (median strategy CS/CSR; Figure 6e,g,h). Indeed, the dual emphasis on salt tolerance, a stress response and managing stormwater volumes, a service more associated with acquisitive species (see Section 4.2), in design manuals from these climates may actually drive the bias we observe (CA1, Figure 3). This would make it a kind of adaptive strategy compromise between design goals associated with competitiveness and stress tolerance, a practical solution to a multifaceted problem. Although compromise planting solutions of this kind may be a way to foster multifunctionality, care needs to be taken to ensure we do not create GSI that are jacks of all trades, but masters of none (Schifman et al., 2017).

4.4 | Relaxing anti-ruderal biasing

4.4.1 | Designed, novel ecosystems

Although the ongoing struggle with weedy plants is a prominent theme in biofilter design manuals (43% of references under the selection criteria 'invasive' reflect concerns about nuisance weeds; Figure 2), there is an emerging school of thought that promotes ruderal-forward GSI as self-sustaining systems that are both designed and novel (Dunnett, 2015). Traditional GSI tends to lie towards the designed ecosystem paradigm, whereby intensive intervention fosters intentional services profiles that must be maintained (i.e. in line with the survivorship mentality noted above). On the other end of the spectrum lie novel ecosystems, which arise from inadvertent human activity and self-sustain without regular management (an example being urban brownfields; Collier, 2015) (Higgs, 2016).

Designed, novel ecosystems fall somewhere in-between, an exciting premise that aims to create systems that are intentional (i.e. with purposeful plant selection and services goals) but expected to be dynamic and self-sustaining, acknowledging that plants and their services may change over time (Dunnett, 2015). Ruderals are expected to play an important role in designed, novel ecosystems, given their ability to colonize and re-colonize space, providing a means for green infrastructure to self-repair; cast in this light, ruderals become a way to preserve plant cover when competitive or stress tolerant plants die, providing a gap filling service with tangible benefits that makes them more than just 'weeds' (Dunnett, 2015; Vanstockem et al., 2019). This is not to say that we want to turn a blind eye to gap dynamics and let all pioneer species (invasive or otherwise) take root in biofilters, rather that there may be value in anticipating and planning for such dynamics, perhaps by populating biofilter seed banks with desirable ruderals (including annuals; see Vanstockem et al., 2018) that self-seed once established (Dunnett, 2015; Koppler et al., 2014). A variety of commercially available biofilter seed mixes exist that might be modified and used for this purpose, and most design guidelines allow for application of seed provided container plants are used to

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establish an initial vegetation presence (MSM Wiki, 2003, SoCal LID, 2010).

4.4.2 | Biodiversity, aesthetics and other associated services

Ruderal species tend to enhance biodiversity in GSI, opposing the tendency towards monoculture typical of competitive dominants. The biodiversity value of predominantly ruderal GSI has been recognized by nature conservation agencies (see, e.g., the Sharrow School green roof in the UK; Dunnett, 2015), and the capacity of ruderal greenspace to enhance biodiversity in urban areas, supporting different species assemblages at different stages of ecological succession, is well established (Braaker et al., 2017; Mathey et al., 2015). Furthermore, although ruderal plants are not always aesthetically perceived (Loder, 2014), many ruderals (particularly annuals) are floriferous, producing attractive multicolor displays that if sufficiently self-seeding could provide recurrent aesthetic value (Dunnett, 2015; Hoyle et al., 2018). Cues to care, interpretive signage and other strategies for furthering the development of an ecological aesthetic may also serve to make ruderals more palatable from a cultural services perspective (Gobster et al., 2007; Nassauer, 1995; Rippy et al., 2022). This leaves concerns regarding dynamicity (and its uncertain consequences) as the principal barrier to relaxing anti-ruderal bias. This barrier too, however, is surmountable, and may be poised to fall, as evidenced by the more permissive stance towards volunteer plants recently adopted in Phoenix, Arizona's green infrastructure handbook: '*Volunteers are generally acceptable unless they interfere with the overall performance of the GI facility. While the resultant naturalized landscape appearance may be less "manicured" than current practices, it should gain overall acceptance as the benefits of GI become known to the public and maintenance managers*'. (Phoenix Metro GI, 2019, p. 62).

5 | CONCLUSIONS AND FUTURE RESEARCH NEEDS

Returning to the three questions posed at the beginning of this study, our work suggests the following answers: (1) biofilter plants are principally selected based on growth form/traits, to survive difficult design conditions, address concerns pertaining to water availability and climate extremes and provide co-benefits such as aesthetics (Figure 2); (2) median adaptive strategies of biofilter plants are biased relative to native plants and wetland-adapted native plants in each climate zone (i.e. towards strategies that are more stress tolerant or competitive than ruderal, depending on the climate zone; Figure 6) and (3) the dominant pattern in adaptive strategy bias observed for biofilter plants across climate zones is not evident for native plants more generally, and appears to be consistent with plant selection practices informed by water availability and climate concerns (i.e. biofilter plants tend to be more stress tolerant (red) and less competitive or ruderal (blue) in climate zones where concerns about water availability, drought and temperature extremes loom large; Figure 7a). In short, the answer to the original overarching question we propose in this paper appears to be yes; present plant selection practices can have unintended consequences for plant adaptive strategy that have the potential to impact the provisioning of ecosystem services by biofilters.

A desire for vegetative permanence in each climate zone, regardless of meteorological conditions, may underly the adaptive strategy biases we observe, as ruderal plants with transient life histories (including annuals) were rarely advocated, but not precluded on a strictly climatological basis. This suggests that biofilter palettes more permissive of ruderals are possible, which would allow future biofilters to be designed for self-repair, facilitating their transition towards designed, novel ecosystems.

Although we have been careful to ensure that the findings reported above are statistically robust, its important to remember that our ability to classify biofilter plants to adaptive strategy was limited by the availability of leaf trait information (leaf area, specific leaf area and leaf dry matter content). Only 32% of listed plants could be classified, and while this subset did not appear to be biased (i.e. favouring certain growth forms over others in ways likely to impact estimates of median plant strategy by climate zone; Figure 5), the only way to know for sure is to develop a more thorough accounting of leaf traits for biofilter species to fuel such analyses. We feel it is important to draw attention to this as a future research need.

In truth, however, it is not only leaf traits that we need a more through accounting of. We also require more information about below-ground traits, about which much less is known. Below-ground traits contribute to a plants adaptive strategy in ways that can sometimes mirror leaf traits; For instance, there exists a root economic spectrum analogous to the worldwide leaf economic spectrum already accounted for by CSR types (Freschet et al., 2012; Roumet et al., 2016), and the two are brought together via the fast-slow plant economic spectrum, which recognizes acquisitive versus conservative trade-offs across all plant organs (Reich, 2014). However, there are exceptions to consider where the economics of different organs do not coincide (Baraloto et al., 2010; Roumet et al., 2016), as well as ways in which CSR-typing based on leaves might miss important below-ground influences entirely. An example of the latter might be the recent recognition of a complete root economic space, wherein the root economic spectrum (which at least has some corollary to leaves) is actually a pattern of secondary importance; the degree of fungal collaborations with mycorrhizae, which may have important implications for nutrient assimilation, among other services of interest, emerged as the principal below-ground pattern (Bergmann et al., 2020; Freschet et al., 2021). Given this, we anticipate that adopting a more whole-of-plant perspective when evaluating CSR in biofilters will be valuable and wish to call attention to this research need.

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Finally, although our work identifies clear adaptive strategy biases in biofilter plant lists, the extent to which plant selection in built infrastructure mirrors, amplifies, or reduces these biases, is unclear. Put another way, we presently lack information on the nature of the primary stress/disturbance filter in biofilters and how that filter might shape realized plant communities. Future work evaluating adaptive strategy profiles in built biofilters and how those profiles change over time (comparable to recent work on urban green roofs) is necessary to characterize the true extent of adaptive strategy bias in built infrastructure and its effect on the ecosystem services that can be provided to people.

AUTHOR CONTRIBUTIONS

Lauren Krauss: Data curation, Formal analysis, Visualization, Writing – Review and Editing; Megan A Rippy: Conceptualization, Methodology, Formal analysis, Writing – Original Draft Preparation.

ACKNOWLEDGEMENTS

This work was supported by an NSF Growing Convergence Research award (NSF #2021015).

CONFLICT OF INTEREST

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

Adaptive strategies for all plants classified and used in this study are reported in two supplemental tables, with appropriate references (Table S2: biofilter plant species; and Table S3: native and native wetland plant species). This information has also been archived in Data Dryad: Rippy and Krauss (2022) Adaptive strategy biases in engineered ecosystems: Implications for plant community dynamics and the provisioning of ecosystem services to people. Dryad, Dataset, https://doi.org/10.5061/dryad.08kprr55t.

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How to cite this article: Krauss, L., & Rippy, M. A. (2022). Adaptive strategy biases in engineered ecosystems: Implications for plant community dynamics and the provisioning of ecosystem services to people. *People and Nature*, *4*, 1644–1663. https://doi.org/10.1002/pan3.10413

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