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Constraining invader dominance: Effects of repeated herbicidal management and environmental factors on curlyleaf pondweed dynamics in 50 Minnesota lakes

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Abstract

1. Curlyleaf pondweed (*Potamogeton crispus*) is one of the most widespread and widely managed aquatic invasive plants in North America. Despite decades of management, the efficacy of long-term management strategies and the effects of environmental drivers on curlyleaf pondweed populations remain uncertain.
2. To evaluate the effects of management and environmental factors on within-lake distribution and local density of curlyleaf pondweed, we collated monitoring data from point–intercept surveys collected by a variety of lake managers across Minnesota, U.S.A. Using this dataset, comprising 177 lake-years of plant data, we examined the influence of herbicide treatment, water clarity, snow depth, and ice cover duration on curlyleaf pondweed distribution and density between 2006 and 2015.
3. We evaluated the effects of herbicides on curlyleaf pondweed at three time points relative to treatment: within year, carryover effects the following year, and cumulative effects over multiple years of treatment. All three temporal measures were associated with significant reductions of curlyleaf pondweed. Additionally, herbicidal management reduced both the density and distribution of curlyleaf pondweed. Given that herbicide management led to reductions that carried over into future years, managers may be able to design multi-year treatments to reduce total management effort over time.
4. We also found strong effects of environmental conditions on curlyleaf pondweed. Elevated lake productivity and decreased winter snow cover were associated with increased springtime distributions of curlyleaf pondweed, whereas duration of winter ice cover had no influence. The influence of productivity suggests that reductions of this invasive species may be an ancillary benefit of water-quality improvements that lower lakes' trophic status. Our results also show that decreased winter snow cover, as predicted under climate change, could exacerbate problematic growth of curlyleaf pondweed.

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5. Harnessing monitoring data from multiple projects, as this study does, allows for robust inference about environmental and management constraints on macrophytes. Because of environmental and management variability, we suggest that treatment regimens follow an adaptive management cycle, with outcomes of management monitored and evaluated, and strategies updated accordingly. It is also vital to continue monitoring both managed and unmanaged lakes to enable stronger inferences about treatment effectiveness.

KEYWORDS

climate change, herbicide, invasive species, macrophyte, winter severity

1 | INTRODUCTION

Aquatic invasive species are one of the primary causes of degradation of freshwater ecosystems (Gallardo, Clavero, Sánchez, & Vilà, 2016), and aquatic invasive plants cause significant ecological and economic impacts (Hussner et al., 2017). Over $100 million is spent annually on control of aquatic invasive plants in the U.S.A. (Pimentel, Zuniga, & Morrison, 2005), yet the ability of those efforts to meet management goals is often uncertain (Abella, 2014; Kujawa et al., 2017; Nault et al., 2015).

A clear understanding of the factors influencing target species populations is vital for helping managers achieve effective and predictable outcomes. Where a factor falls within managers' control, it can be adjusted to maximise desired outcomes. For example, the timing of herbicide applications or biomass removal treatments can be adjusted to maximise impacts on plant energy reserves (Sukhodolova, 2017). Conversely, factors beyond the control of managers can be understood in order to account for their influence on management outcomes and potentially enable managers to adapt to such influence. For example, managers might consider how environmental conditions affect the baseline abundance of invasive species in systems they manage, allowing prioritisation of management that is most likely to achieve desired goals (Latzka, Hansen, Kornis, Van Der Zanden, & Peters, 2016). By optimising the factors they can control, managers can maximise efficacy of management. By accounting for factors beyond their control, managers can increase predictability of outcomes. To improve the management of an invasive aquatic plant that is widely targeted in Minnesota, U.S.A., we evaluated and quantified the influence of key factors—both inside and outside the domain of managers' control—on the outcomes of control efforts.

Using monitoring data collected over a decade of management, we assessed how treatment and environmental factors influenced the population dynamics of curlyleaf pondweed (*Potamogeton crispus* L.; hereafter, CLP). Curlyleaf pondweed is one of the most widespread and problematic aquatic invasive plants in North America and is a nuisance invader in much of the world (Bolduan, Van Eeckhout, Quade, & Gannon, 1994). In Minnesota, CLP has been present for over a century and has been found in >730 lakes (Valley & Heiskary, 2012), where concerns about displacement of native species (Bolduan et al., 1994), impacts on water quality (James, Dechamps, Turyk, & McGinley, 2007), and recreational interference (Valley & Heiskary, 2012) have resulted in extensive control efforts in many lakes.

Curlyleaf pondweed behaves as a winter annual in Minnesota (Johnson, Jones, & Newman, 2012; Valley & Heiskary, 2012), sprouting from asexual reproductive structures called turions in the autumn when water temperatures drop below 20°C (Bolduan et al., 1994; Sastroutomo, 1981; Tobiessen & Snow, 1984). In the spring, when water temperatures reach 11°C, overwintered CLP plants begin to grow rapidly before most native macrophyte species are active (Woolf & Madsen, 2003). This period of active CLP growth during native macrophyte dormancy has proven an effective time for selectively targeting CLP with herbicides (Johnson et al., 2012; Jones, Johnson, & Newman, 2012; Netherland, Skogerboe, Owens, & Madsen, 2000; Skogerboe, Poovey, & Getsinger, 2008). Finally, CLP produces new turions and senesces in early summer when water temperatures surpass 25°C (Bolduan et al., 1994; Chambers, Spence, & Weeks, 1985; Heiskary & Valley, 2012; Johnson et al., 2012; Woolf & Madsen, 2003). By targeting CLP management before the plants produce the next generation of turions, management has the potential to achieve population-level reductions that last multiple years (Johnson et al., 2012; Skogerboe et al., 2008).

Despite decades of management efforts and accumulation of knowledge of CLP ecology and treatment, there remains significant uncertainty regarding expected outcomes of management. This uncertainty is reflected in shifting guidance for management, and even reversals of recommendations as new findings have been reported. For example, determining how many consecutive years CLP management should be conducted to reduce populations and reproductive output has been elusive. Two to 4 consecutive years of herbicide treatment have been suggested as optimal because of diminishing returns on reductions of CLP distribution, biomass, and turion abundance (Johnson et al., 2012; Skogerboe et al., 2008). However, other studies have reported that, even after 7 years of management, CLP remained abundant enough to require ongoing intervention to meet management goals (McComas, Christianson, &

Singh, 2015). Although many studies have suggested that multiple years of treatment are vital for maintaining CLP control (Johnson et al., 2012; McComas et al., 2015; Poovey, Skogerboe, & Owens, 2002; Skogerboe et al., 2008), there has been little quantification of optimal long-term control strategies.

The relationship between CLP and lake productivity is another area of uncertainty. Initial studies found that CLP dominance was associated with high-productivity lakes (Nichols & Shaw, 1986; Tobiessen & Snow, 1984). Later, the possibility that internal nutrient loading driven by CLP's early-summer senescence was a driver of high-productivity led managers to pursue CLP control as a water-quality improvement strategy (Bolduan et al., 1994; James, Barko, Eakin, & Sorge, 2002). Alternatively, CLP may simply be well-adapted for growth in nutrient-rich lakes, rather than driving nutrient loading, and subsequent studies showed high context dependency of the senescence-productivity relationship, which led to water-quality enhancement being questioned as a rationale for control (Heiskary & Valley, 2012; Johnson et al., 2012; McComas et al., 2015).

A third area of uncertainty concerns the relationship between overwintering conditions and inter-annual variability in CLP abundance. Recent work has shown that overwintering conditions are likely to influence annual fluctuations in CLP populations in unmanaged lakes in Minnesota (Valley & Heiskary, 2012). However, it remains unknown how these annual fluctuations interact with management in treated lakes (Valley & Heiskary, 2012).

These areas of uncertainty, and resulting lack of clear guidance to managers aiming to control CLP (e.g. how to best design a control plan for multi-year reductions, or how winter conditions will mediate control effectiveness), arise at least partly due to research on CLP biology and management having mainly comprised small-scale and case studies. Integration and analysis of larger datasets across greater spatial and temporal scales would allow more robust inferences and generalisations to be made (Frater et al., 2016; Kujawa et al., 2017; Nault et al., 2017). Even if implementing treatments based on existing science, managers face challenges such as variable outcomes (Kujawa et al., 2017), uncertainty regarding best practices (Hussner et al., 2017), and a lack of coordination and sharing of accumulated data and knowledge (c.f. Kujawa et al., 2017). Retrospective analysis of monitoring data collected during management of aquatic invasive plants offers a means to address these gaps (Heger et al., 2013). Such data can be collated and analysed to evaluate management practices at broader scales to advance understanding and practices (Fleming & Dibble, 2015; Frater et al., 2016; Heiskary & Valley, 2012; Hussner et al., 2017; Kujawa et al., 2017; Valley & Heiskary, 2012).

In Minnesota, dozens of management organisations supervise or monitor treatment of CLP in hundreds of lakes, but most projects are only evaluated at the scale of one to a few lakes, limiting capacity for adaptive management through broader learning and re-adjustment of strategies (Abella, 2014). By integrating across projects, synthetic analyses can capitalise on large-scale variation in factors that influence CLP distribution, density, and control efforts in established populations, enabling more general understanding of factors influencing treatment outcomes. For example, landscape-level analyses can identify and quantify interactions between management and variation in water chemistry (Frater et al., 2016). Because of variation in management strategies used, broadscale analyses also enable the efficacy of alternative management approaches to be compared (e.g. variation in the timing of first management interventions relative to initial invasion (Kujawa et al., 2017)).

Using a retrospective analysis of data collected by lake managers from 2006 to 2015, we evaluated the effects of herbicide-based management, lake productivity, and winter conditions on lake-level CLP distribution and density. The power of the dataset we have compiled draws from both the consistency of the methods used for monitoring and the extent of the data across space, time, and management strategies. To understand how managers can optimise herbicide treatment over multiple years, the effects of management were examined over three temporal windows: within the year of treatment (within-year), in the year following treatment (carryover), and as an accumulation of consecutive years of treatment (consecutive). To understand how environmental factors affect CLP, and how managers can adapt strategies based on these factors, we assessed the influence of lake productivity and winter conditions on CLP populations. Based on our findings, we offer recommendations for how managers can (1) optimise management with respect to number of years of consecutive treatment, and (2) incorporate natural background variation in CLP populations into planning and evaluation of management efforts.

2 | METHODS

2.1 | Data collation

With the aid of Minnesota Department of Natural Resources (MNDNR) staff, we identified 12 lake management organisations, including consultants, state agencies, local government units, and researchers, known to have conducted plant surveys that would include CLP. From each organisation, we requested datasets that included point–intercept survey data with at least one survey in spring or early summer (to capture CLP growth prior to summer senescence). The point–intercept survey method allows comparison across lakes while controlling for variation in sampling effort and has been widely adopted as the predominant sampling method for aquatic plant management (Madsen, 1999; Madsen & Wersal, 2017). Survey data from these sources were combined with data obtained from previously published research (Johnson et al., 2012; Jones et al., 2012), ongoing research from the Riley–Purgatory Bluff Creek Watershed District (R.M. Newman, unpublished data), and lakes from the MNDNR Sentinel Lakes In a Changing Environment (SLICE) programme (https://www.dnr.state.mn.us/fisheries/slice/sentinel.html). We assembled and organised all data at the survey-point level to ensure that statistics (e.g. frequency of occurrence) were calculated consistently across surveys. The dataset represented lakes spanning a wide latitudinal range within Minnesota, with a higher concentration of lakes closer to the Twin Cities metropolitan area

(Figure 1). From the 12 organisations, and our own past and ongoing research projects, a total of 575 surveys from 67 lakes were acquired. Of those 67 lakes, 50 lakes included data for all variables of interest and surveys covering either April/May (early surveys, *n* = 101 surveys) or June (late surveys, *n* = 145 surveys; Table 1). In total, our dataset comprised 177 lake-years, including 104 untreated lake-years and 73 treated lake-years.

Aquatic plant management targets two properties of a target species within a lake: the distribution or areal extent of the species and its density where present. Typically, studies quantifying management and environmental effects using observational datasets have focused on the former, using proportion of occupied sampling locations (frequency of occurrence) to quantify population changes (Heiskary & Valley, 2012; Kujawa et al., 2017). The experimental standard for density, biomass, is rarely collected during lake management monitoring, but many surveyors do record ordinal data of plant density on sampling rakes during point–intercept surveys. These rake densities are a subjective, visual assessment of the amount of each species recovered at a sampling point (Deppe & Lathrop, 1992; Hauxwell et al., 2010; Perleberg, Radomski, Simon, Carlson, & Knopik, 2016). Although different scales have been used (1–3, 1–4, 1–5) we limited use of density data to surveys collected using a 1–4 rake coverage scale, with 1 being low density (one or a few stems) and 4 being high density (overflowing the sampling rake). Although the rake density method is subjective, it is nonetheless useful as a semi-quantitative, relative density measure that requires little additional effort (Deppe & Lathrop, 1992; Hauxwell et al., 2010; Madsen & Wersal, 2017; Valley et al., 2015). We used these data to evaluate

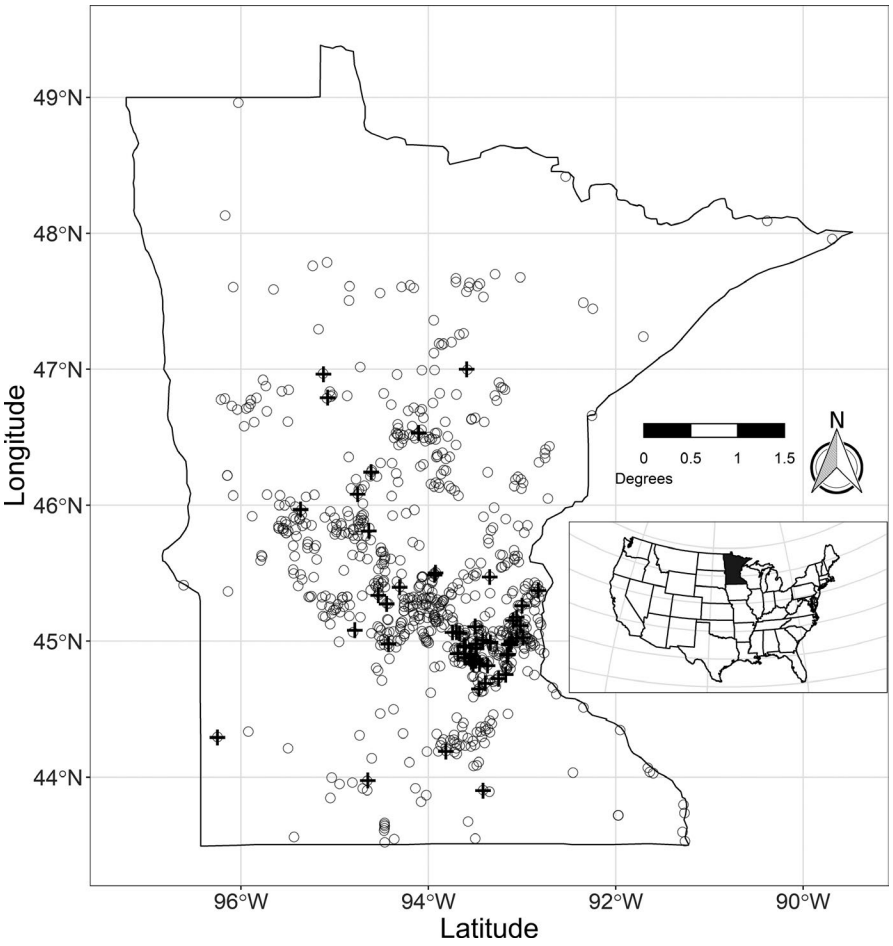


FIGURE 1 Distribution of lakes with known occurrences of *Potamogeton crispus* in Minnesota (dots) and lakes included in this study (crosses)

TABLE 1 Number of lakes, lake-years, and point–intercept surveys that were compiled and used in this study

	n lakes	Treated?	*n* lake-years	Treated?	*n* late surveys	Treated?	*n* early surveys	Treated?
Frequency of occurrence	50	Yes = 22 No = 42	177	Yes = 73 No = 104	145	Yes = 63 No = 82	101	Yes = 48 No = 53
Mean rake density	28	Yes = 16 No = 20	91	Yes = 49 No = 42	80	Yes = 40 No = 40	63	Yes = 35 No = 28

Note: Sample sizes are split by early (April/May) and late (June) survey periods and by whether lakes were or were not treated with herbicide for curlyleaf pondweed control.

changes in CLP density for the subset of surveys in which it was recorded.

For each survey, CLP frequency of occurrence and mean rake density were calculated (hereafter, frequency and density, respectively). Frequency for a survey was calculated as the number of points at depths ≤4.6 m where CLP was detected, divided by the total number of points sampled within that zone (Johnson et al., 2012; Jones et al., 2012; Kujawa et al., 2017; Valley & Heiskary, 2012). To ensure that we were not introducing bias into our dataset through the use of a 4.6-m cut-off depth for survey data, we evaluated three alternative cut-offs using a subset of the data (Table S1 and S2): 4.6 m, which is the depth zone used by MNDNR and previous studies (Johnson et al., 2012; Valley & Heiskary, 2012); a lake-specific littoral depth (2 × the maximum Secchi depth observed for each lake); and no cut-off (including all survey points). These three thresholds did not produce qualitatively different patterns for our statistical analyses (Figures S1–S3 and Table S3). This evaluation showed that (1) the cut-off used needs to be chosen to ensure that all vegetated depths are included in the analysis, and (2) each lake needs to be treated the same through time. If both of these criteria are met, differing cut-off points may alter absolute numeric values produced from an analysis, but will not change qualitative patterns, i.e. relative differences between lakes or across time will remain consistent. We report results with the cut-off of 4.6 m to facilitate comparison to past research (Johnson et al., 2012; Valley & Heiskary, 2012). For the surveys that had density data, we computed the mean of rake density ratings for points with CLP (i.e. excluding absences), providing a measure of relative density where CLP occurred.

We categorised surveys as representing one of two time periods. First, surveys conducted during April or May (hereafter, early survey) were typically conducted at water temperatures <10°C. Early surveys reflect pre-treatment conditions in lakes to be treated and typically take place prior to rapid spring growth of CLP. Second, surveys conducted in June (hereafter, late survey) were typically conducted when water temperatures were 16–21°C. Late surveys represent post-treatment conditions in managed lake-years and occur close to the period of peak CLP biomass prior to summer senescence, which is *late* with respect to the annual life cycle of the species.

Treatment and environmental data were gathered for each lake-year for which we had survey data. For each year, each lake was classified as having been treated (herbicide applied as part of a lake-level effort to control CLP growth) or untreated (no large-scale or offshore treatments targeting CLP) based on MNDNR permitting database records. Herbicide treatments were typically conducted using early-season, low-dose applications of contact herbicides (e.g. endothall [7-oxabicyclo[2.2.1]heptane-2-3dicarboxylic acid] and diquat [6,7-dihydrodipyrido (1,2-a:2′,1′-c) pyrazinediium dibromide]; Bugbee, Gibbons, & June-Wells, 2015; Getsinger, Netherland, Grue, & Koschnick, 2008; Skogerboe et al., 2008), but some lakes in the dataset were also treated concurrently for other species or using other methods, e.g. mechanical harvesting (n = 17 lake-years). If a lake received CLP treatment in a year, we assumed the treatment occurred after the early survey and before the late survey. This allowed evaluation of (1) within-year effects using late-survey comparisons between treated and untreated lakes and (2) carryover effects using early-survey comparisons between lakes that were treated versus untreated in the previous year.

Water-quality data were obtained from the Minnesota Pollution Control Agency (https://cf.pca.state.mn.us/water/watershedweb/wdip). The previous year's August Secchi depth was chosen as a proxy for lake productivity (Read et al., 2017). Secchi data from the previous August were used for three reasons. First, data for other metrics of productivity, such as trophic state index or total phosphorus measurements were sparsely available. Second, the early-season senescence of CLP means that Secchi data from the year of treatment represent conditions after CLP has entered a summer dormancy period (Secchi readings are typically taken in July–September), whereas previous August Secchi depth represents water clarity conditions in which CLP sprouting and initial growth occurred. Third, CLP has been implicated as a driver of internal loading of phosphorus (Heiskary & Valley, 2012; James et al., 2007), so use of previous years' water-quality measurements minimises potentially confounding effects of phosphorus loading driven by CLP senescence.

Data for snow depth and duration of ice cover were obtained from MNDNR's Minnesota State Climatology Office (https://www.dnr.state.mn.us/ice_out/index.html). Ice cover was calculated as the number of continuous days that a lake was covered with ice in the winter prior to each survey. Snow cover was calculated as the mean daily snow depth over the ice-covered period at the nearest National Weather Service Reporting station (Valley & Heiskary, 2012). Although these stations vary in proximity to each lake (min = 1.2 km, max = 36.9 km, mean = 13.1 km), the data are consistently and reliably gathered and are best available indicators of snow cover across the region over time.

In sum, we calculated a CLP frequency statistic (and density statistic where available) for each early and late survey, which was paired with annual data for treatment (binary: treated/untreated), number of consecutive years of treatment, previous August Secchi depth, previous winter ice cover, and previous winter snow depth. Sample sizes for each survey period (early and late), numbers of treated and untreated lakes, and summary statistics for all variables are presented in Tables 1 and 2, respectively. Sample sizes for each survey (n = 246) are shown in Data S1.

2.2 | Data analysis

Generalised linear mixed-effects models were used to assess the influence of herbicide treatment, previous August Secchi depth, snow cover, and ice cover as main effects on CLP frequency and density. Lake was assigned as a random effect to account for repeated sampling at the lake level (Colegrave & Ruxton, 2017; Valley & Heiskary, 2012), and an observation-level random effect was also estimated to account for overdispersion of frequency data (Harrison, 2015). Models were developed by first testing for interactions between treatment and environmental variables. Where significant interactions were found, the interaction term was retained and the effect

TABLE 2 Mean and standard deviation (*SD*) for all variables used in this study, grouped by lake-years that were treated (n = 73) or not treated (n = 104) for curlyleaf pondweed

	Survey time period	Frequency of occurrence		Mean rake density		Number of consecutive years of treatment		Previous August Secchi clarity (m)		Mean daily winter snow depth (cm)		Ice cover duration (days)	
		Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Treated lake-years	Early	0.29	0.22	1.25	0.27	1.17	1.24	1.00	0.64	35.46	20.74	134.81	14.94
	Late	0.13	0.13	1.32	0.54	1.46	1.73	0.86	0.57	32.64	21.41	134.00	13.55
Untreated lake-years	Early	0.45	0.25	1.95	0.84	NA	NA	1.12	0.75	32.02	22.15	132.11	14.18
	Late	0.32	0.27	1.90	0.71	NA	NA	1.43	1.27	38.69	23.85	134.00	14.08

Note: Values represent mean values of each variable from 50 Minnesota lakes in years that were monitored for curlyleaf pondweed growth from 2006 to 2015 during early (April/May) and late (June) time periods.

of the environmental variable was estimated separately for treated and untreated groups; non-significant interactions were dropped from models. Using these models, each explanatory term was tested against the null hypothesis that it had no effect on the response variable when holding other variables constant (at mean values for snow, ice cover, and previous August Secchi depth; untreated for treatment state; and zero for cumulative years of treatment). Because early and late surveys corresponded to pre- and post-treatment conditions, respectively, we differentiated within-year, carryover, and consecutive-year treatment effects. In treated lakes, late surveys were used to estimate within-year effects (CLP conditions following treatment) and early surveys to estimate carryover effects (CLP conditions in the subsequent spring following treatment). For lakes receiving multiple consecutive years of treatment, an additional effect of cumulative treatment years was estimated.

To assess factors influencing CLP frequency (which is a proportional value bounded between 0 and 1), we used a generalised linear model with a binomially distributed response, resulting in parameter estimates on the log-odds or logit scale of the response variable (Table 3; Crawley, 2005). Prior to analysis, snow depth, ice cover, and previous August Secchi depth were centred at dataset mean values and scaled by dividing by the standard deviation of each respective variable to ensure comparability of directionality and magnitude of estimated effects. Model results were then back-transformed for interpretation and visualisation. All estimates and standard errors reported are among-group values, and variance at the group (lake) level is available in Data S1. We used a similar approach to analyse factors affecting CLP density. We modelled density using a generalised linear model with γ-distributed errors to ensure accommodation of the bounded response (on a 1–4 scale; Crawley, 2007).

In lakes with multi-year treatments, we estimated the annual change in treatment area as a function of consecutive years of treatment using a linear mixed-effect model with lake as a random effect. To evaluate the possibility that late-season results were biased by the effects of winter snow cover on early-season survey abundances, we used linear regression to test the relationship between winter snow cover and treatment effort (proportion of the lake area <4.6 m deep permitted for treatment).

Analyses were conducted in R 3.6.1 (R Core Team, 2019), and models were tested using the lme4 package (*v1.1-18-1*, Bates, Maechler, Bolker, & Walker, 2015); additional packages used in data manipulation, analyses, and visualisation inlcude DATA.TABLE, DPLYR, GGMAP, GGPLOT2, MAPDATA, NUMDERIV, and SF (Becker, Wilks & Brownrigg, 2018; Dowle & Srinivasan, 2019; Gilbert & Varadhan, 2019; Kahle and Wickham, 2013; Pebesma, 2018; Wickham, 2016; Wickham, François, Henry & Müller, 2019). All analyses and dataset development code are available in Data S1.

3 | RESULTS

Overall, both herbicide treatments and environmental conditions influenced frequency and density of CLP (Table 3). There were

TABLE 3 Generalised linear mixed-effects models of curlyleaf pondweed frequency of occurrence and mean rake density with lake as a random effect (n = 50 and n = 28 for frequency of occurrence and mean rake density models, respectively)

Response	Survey period	Explanatory variable	Estimate	Standard error	p-Value
Frequency of occurrence	Early	Untreated (last spring)	**−0.565**	0.216	0.009
		Treated (last spring)[a]	−0.219	0.236	0.353
		Cumulative years treated	**−0.529**	0.117	<0.001
		Previous August Secchi[b]	**−0.465**	0.205	0.023
		Snow[b]	**−0.509**	0.114	<0.001
		Ice cover[b]	−0.009	0.104	0.931
	Late	Untreated	**−1.034**	0.268	<0.001
		Treated[a]	**−1.086**	0.390	0.005
		Cumulative years treated	**−0.300**	0.145	0.039
		Untreated: previous August Secchi[b]	**−0.546**	0.186	0.003
		Untreated: snow[b]	−0.143	0.164	0.384
		Ice cover[b]	−0.127	0.144	0.377
		Treated: previous August Secchi[a,b,c]	**1.146**	0.480	0.017
		Treated: snow[a,b]	**0.718**	0.273	0.008
Mean rake density	Early	Untreated (last spring)	**0.525**	0.089	<0.001
		Treated (last spring)[a]	**−0.219**	0.071	0.002
		Cumulative years treated	−0.031	0.031	0.314
		Previous August Secchi[b]	**−0.137**	0.069	0.047
		Snow[b]	−0.011	0.038	0.768
		Ice cover[b]	−0.051	0.033	0.123
	Late	Untreated	**0.634**	0.080	<0.001
		Treated[a]	**−0.414**	0.100	<0.001
		Cumulative years treated	−0.041	0.033	0.211
		Previous August Secchi[b]	−0.048	0.044	0.269
		Snow[b]	−0.083	0.043	0.057
		Ice cover[b]	0.001	0.047	0.980

Note: Estimates are given on the logit and log scales of the response variable for frequency and density, respectively (only relative magnitudes, directionality, and significance are easily interpretable from model estimates; Figures 2 and 3 show relationships on untransformed scales). Only significant ($p \leq 0.05$) interactions between treatment and environmental parameters are shown. Bold font indicates parameters that are significant ($p \leq 0.05$) relative to a null relationship to the linear predictor scale.

[a]Δ from untreated group.

[b]Indicates variable was transformed by centring on dataset mean and scaled by variance.

[c]Slope is significantly different from untreated group, but not significantly different from zero.

significant treatment effects across both survey periods (early, late) and both response variables (frequency and density); environmental conditions had stronger effects on frequency than density (Table 3). There were also significant interactions between treatment and environmental variables (for late-survey frequency; Table 3 and Figure 3). Higher prior-year August Secchi depths (i.e. lower productivity) were associated with declines in CLP frequency. Greater snow cover was also found to be strongly associated with lower CLP frequency. Ice cover was not a significant predictor of CLP frequency. Herbicide treatment significantly reduced CLP density, but most environmental variables showed no significant relationships with density (with the exception of a marginally significant, negative effect of previous August Secchi depth).

3.1 | Herbicide treatment

Herbicide treatment reduced CLP in multiple ways. Late-survey data showed a within-year reduction in mean frequency of 0.25 relative to the untreated group (Tables 2 and 3 and Figure 2). We observed no significant carryover effect of treatment on CLP frequency; however, both early and late surveys revealed significant negative effects of multiple consecutive years of treatment on frequency (Table 3). There were non-linear, diminishing effects of additional years of treatment based on early surveys. Across the entire range of consecutive years of treatment observed, there was a 0.06 decline per additional year of treatment ($p < 0.001$). However, this effect varied, from a 0.16 decline with 1 additional year of treatment to a 0.02 decline for the fifth

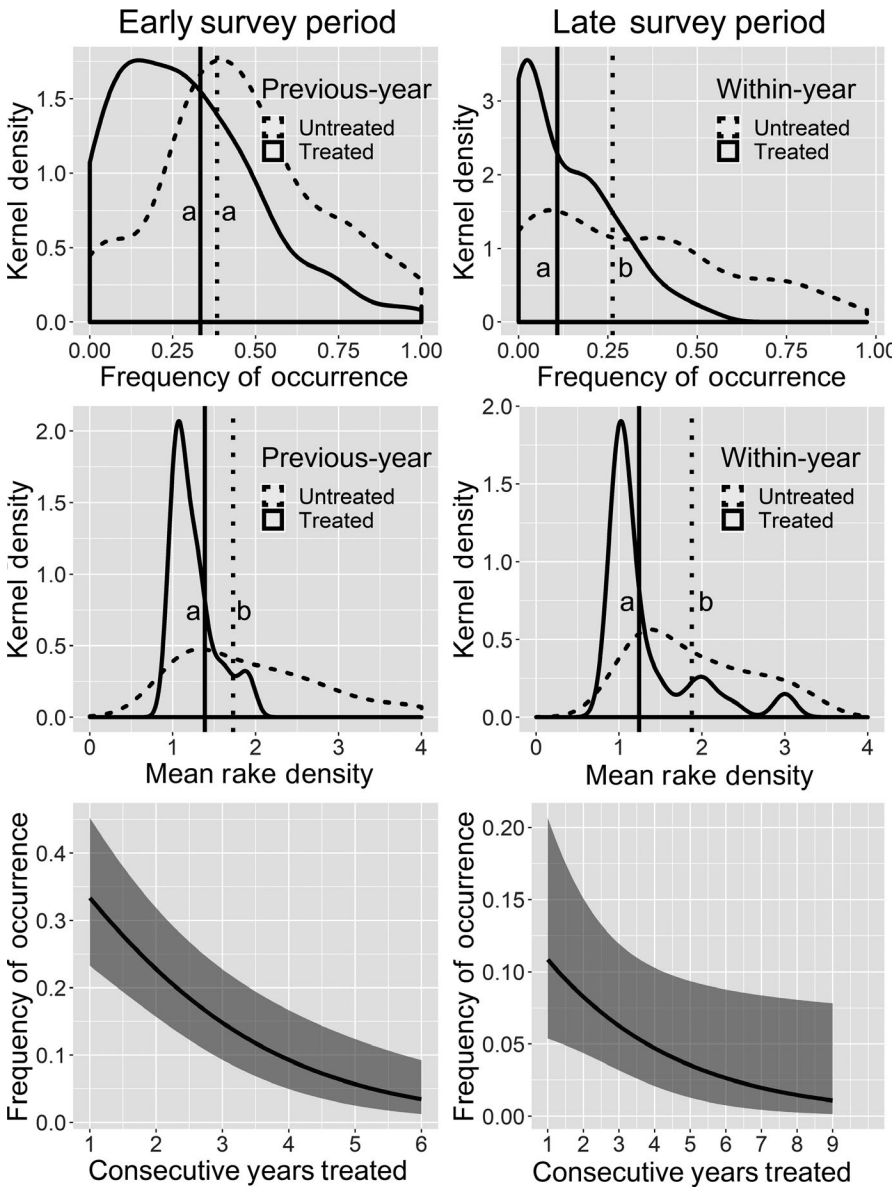


FIGURE 2 Effects of herbicide treatment on early survey (April/May) and late survey (June) *Potamogeton crispus* frequency of occurrence and mean rake density. Previous-year (carryover) treatment effects (left top and left centre panels) and within-year treatment effects (right top and right centre panels) and are shown as kernel density plots, with significant differences ($p \leq 0.05$) between treated (solid lines) and untreated (dashed lines) groups indicated by different letters on vertical lines positioned at group means (minus modelled effects of environmental variables). Effects of consecutive years of treatment and 95% confidence intervals (bottom panels) are represented as lines and shaded regions, respectively. Effects of consecutive years of treatment on mean rake densities were non-significant and are not shown

additional year of treatment (Table 3 and Figure 2). Consecutive years of treatment had less influence on late-survey frequency, with a net decrease across the range of observed consecutive years of 0.01 per additional year of treatment ($p = 0.039$).

We also found that herbicide treatment significantly reduced CLP density. This effect was significant both within-year and as a carryover effect (Table 3) but there was no effect of cumulative years of treatment on densities in either early or late surveys. In sum, within-year herbicide treatment was associated with reduced CLP frequency and density, carryover effects were only associated with decreased density, and consecutive years of treatment were only associated with decreased frequency.

In lakes that were treated for multiple years, the acreage treated in subsequent treatment years declined by 5.5 hectares (±2.2 *SE*) for each additional year of treatment, starting from a first-year mean of 45.1 hectares (±7.7). For treated lakes, greater winter snow cover was not associated with greater treatment effort based on the proportion of the lake area < 4.6 m deep permitted for treatment ($p = 0.23$, $R^2 = 0.031$), suggesting that late-survey results for snow cover were not biased by managers' responses to early-survey CLP distributions.

3.2 | Productivity

Decreasing productivity (i.e. increasing prior-year August Secchi depth) was associated with declines in CLP frequency and density. In early and late surveys, there were significant negative effects of increasing previous August Secchi depth on CLP frequency (Table 3), with a 0.09 decrease in frequency for each additional meter of previous August Secchi depth (Figure 3; mean of treated and untreated groups). In the late-survey data for untreated lakes, CLP frequency significantly declined with increasing previous August Secchi depth. While the treated and untreated groups differed significantly ($p = 0.02$), there was no significant effect of

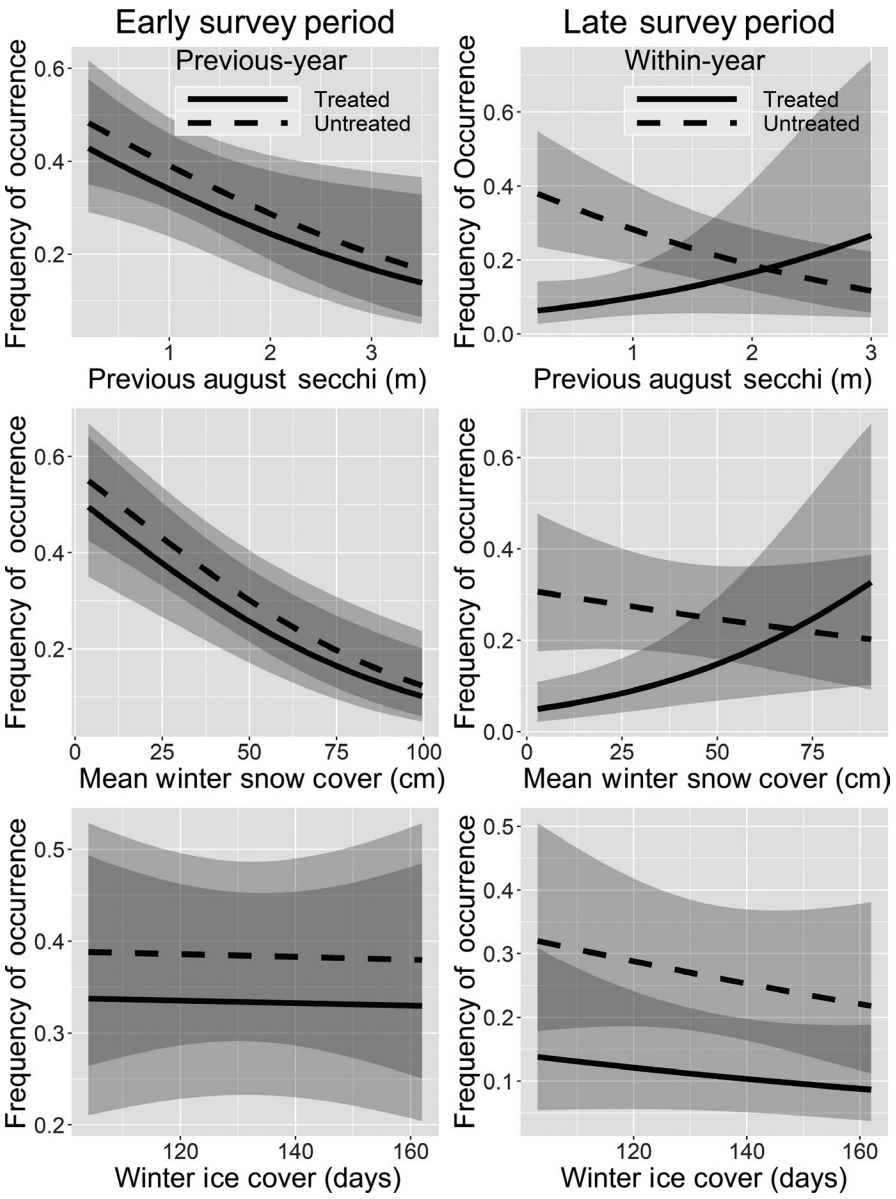


FIGURE 3 Effects of productivity (top panels), mean winter snow depth (centre panels), winter ice cover duration (bottom panels) and treatment (line type) on early (April/May; left panels) and late (June; right panels) *Potamogeton crispus* frequency of occurrence. Dashed lines show modelled relationships for untreated lake-years; solid lines show models for treated lake-years. Shaded regions cover 95% confidence intervals for modelled relationships. The only significant interactions observed between treatment and environmental conditions were late survey frequency × productivity and late survey frequency × snow cover (top right and centre right panels, respectively)

previous August Secchi depth on late-survey frequency in treated lakes (Table 3; Figure 3). Previous August Secchi depth was also the only environmental variable with a significant relationship with density, with which it had a marginally significant negative association based on early surveys.

3.3 | Winter conditions

Ice cover was not a significant predictor of frequency or density in either survey period. Greater winter snow depth was associated with decreased CLP frequency in both early and late surveys, but had no effect on density. For early surveys, frequency declined with increasing winter snow depth from 0.49 to 0.10 for treated lakes, and 0.54 to 0.12 in untreated lakes across the observed range of snow depths (3.8–99.6 cm; Table 3). This equates to an approximately 4% reduction in frequency per dm of additional mean daily snow depth (Figure 3; mean of treated and untreated groups). Late-survey data showed no significant effects of snow depth or ice cover in untreated lakes; however, a significant positive relationship was found between snow depth and frequency in treated lakes (Table 3; Figure 3).

4 | DISCUSSION

Two categories of factors that drive CLP distribution and density within lakes were identified: (1) herbicide treatment variables, which managers can directly control to meet management goals (e.g. by employing multiple consecutive years of treatment to reduce frequency); and (2) environmental drivers, which managers cannot directly control but can potentially adapt to over time and space (e.g. by anticipating nuisance growth in lakes and years with low snow cover).

Herbicide treatment was effective in reducing within-year, in-lake distribution (frequency of occurrence) and local abundance (mean rake density) of CLP. This reinforces prior work showing that early-season endothall treatments were effective for reducing CLP (Johnson et al., 2012; Skogerboe et al., 2008). We did not find a significant carryover effect of herbicide treatment based on early-survey frequency, which departs from the results of previous research (Johnson et al., 2012). However, we did observe a non-significant trend of decreased CLP frequency as a carryover effect. Density was reduced both within-year, and as a carryover effect of treatment. Carryover reduction in CLP from prior treatments has been attributed to reduced reproductive capacity through limitation of turion production (Johnson et al., 2012).

In both early and late surveys, treating for multiple consecutive years produced additional reductions in CLP distribution. The additional effect of consecutive years of treatment on CLP decreased across the range of years represented in our dataset (early surveys = 5-year max.; late surveys = 8-year max.). This could be taken as evidence for a diminishing return of treatment over multiple years (Johnson et al., 2012). However, because treatment is not binary (yes/no) as simplified here, but instead varies in terms of the proportion of the lake area <4.6 m deep treated, managers may choose to continue treatment despite diminishing reduction of remaining CLP. In support of this, as the number of cumulative years of treatment increased, the total area treated declined (Data S1), suggesting that net management effort may be lower where small remaining areas of CLP are persistently targeted. Previous studies have suggested that multi-year treatments are vital to effectively suppress CLP, but a clear understanding regarding how long managers should plan to intervene has been elusive (Johnson et al., 2012; McComas et al., 2015; Poovey et al., 2002; Skogerboe et al., 2008). Despite up to 8 years of treatment being represented in the current dataset, it is difficult to make overarching recommendations because data were depauperate for treatments lasting more than 3 years (lake-years: early surveys, n = 3; late surveys, n = 5). Despite this limitation, we can draw two clear conclusions. First, treating for multiple consecutive years reduced CLP distributions more than treating for a single year did. Second, while absolute change in frequency diminished as consecutive years treated increased, total management effort decreased. Together, these results suggest that employing consecutive treatments may yield carryover benefits. It is critical to adjust such treatments annually to track changes in within-lake distribution of CLP and thereby maximise treatment efficiency and minimise non-target impacts to other organisms.

A crucial unknown is when control efforts should be halted, and how populations will respond to suspension or cessation of treatment (Epanchin-Niell & Hastings, 2010). Unfortunately, across all the surveys compiled for this study, there were few data to address what happened when management ended. This is because monitoring of treated lakes almost always ended when treatment ended. Because turions in sediments act as a means of CLP recovery, we suspect that response to cessation of treatment would be a function of the number of years that the turion bank was able to accumulate countered by the number of years it was exhausted through treatment (Johnson et al., 2012). To optimise long-term management of CLP, the cost of treatment must be balanced with the risk of population recovery when treatment is stopped. More long-term data are needed to quantify these dynamics. We encourage managers to continue to monitor aquatic plant communities, when possible, even after active control efforts have ended.

Previous August Secchi was a significant, positive predictor for all measures of CLP abundance except late-survey density. This aligns with previous research, which has found that eutrophic lakes are associated with greater CLP growth (Bolduan et al., 1994; Heiskary & Valley, 2012). This preference for high-productivity, low-clarity lakes has been attributed to physiological adaptations, including a low-light-compensation point and robust growth under low-light conditions (Tobiessen & Snow, 1984; Wu, Cheng, Liang, He, & Wu, 2009). Our work extends this understanding of CLP tolerance of low-clarity lakes by modelling lake as a random effect. That is, even within individual lakes, more-productive years were followed by increases in early- and late-survey frequency and early-survey density. Thus, lake-specific trends in water quality could be monitored to plan allocation of CLP treatment. For example, as water clarity increases, managers may be able to allocate less effort to CLP management. This also suggests that decreased CLP distributions could be an ancillary benefit of catchment efforts to improve water quality (e.g. nutrient inflow reductions).

Winter snow depth appeared to strongly influence CLP frequency. In early surveys, CLP frequency declined with increasing snow depth, consistent with previous work (Valley & Heiskary, 2012). Our study adds to the strength of this conclusion by including a larger number of lakes and explicitly including treatment as a factor (Valley & Heiskary, 2012: 34 lake-years, one managed lake; our study: 177 lake-years, 22 managed lakes). The decline in early-survey CLP frequency with increasing snow depth was probably due to decreased light available to overwintering plants. Although CLP can photosynthesise under low temperature and light conditions (<1% of surface irradiance), low-light conditions for overwintering plants are nevertheless associated with decreased elongation rates and decreased sprouting from turions (Tobiessen & Snow, 1984; Wu et al., 2009). Ice cover had no significant effect on any of the response variables examined, echoing previous work and reinforcing light limitation by snow cover as the primary driver of winter effects on CLP (Tobiessen & Snow, 1984; Valley & Heiskary, 2012).

We observed a more nuanced influence of snow depth when we considered late surveys and lakes subjected to herbicide treatment. The negative effect of winter snow depth on CLP frequency did not carry through to late surveys in either treated or untreated lakes. Late surveys of untreated lake-years showed a non-significant negative trend between CLP frequency and snow depth, but the treated group showed an unexpected positive correlation (antagonistic interaction) with CLP frequency in treated lake-years. We suspect that this relationship may have been produced by a higher efficacy

of herbicide treatment (relative to untreated lake-years) when snow depth was lower. This is a counterintuitive result that contradicts our expectation that treatments might be most effective in places where environmental factors were concurrently suppressing CLP.

Increased susceptibility of CLP to herbicide management following low snow depth is one potential explanation for this pattern. If low snow cover moved up the timing of spring growth, this could result in CLP being treated at a time when it is more susceptible to herbicide treatments because of depleted energy reserves. Curlyleaf pondweed carbohydrate reserves have been reported to be lowest between January and April (Woolf & Madsen, 2003). At these minima, plants may have less capacity to recover from injury, and thus timing treatments to align with these low points may increase efficacy (Madsen, 1997; Sukhodolova, 2017). Future research should test the generalisability of this result, and evaluate energetics as a potential mechanism underlying increased susceptibility. An alternative explanation for the unexpected increase in treatment efficacy in low snow years is increased management effort. Managers may be identifying CLP populations as being more robust during early surveys following low-snow years and thus prescribing more-aggressive treatments. To evaluate this as a potential artefact in our analysis, we tested whether winter snow cover was associated with greater treatment effort (higher proportion of the lake area < 4.6 m deep permitted for treatment) and found no relationship (p = 0.23, R^2 = 0.031). If the hypothesised energetic mechanism is substantiated, this increased efficacy of treatments in low-snow years could be incorporated into management planning. Managers could exploit years when winter snow cover is low to maximise reductions in within-lake CLP distributions—an effect that our results indicate could carry through to future years of treatment. Managers could also allocate more effort to individual lakes that had lower snow cover. Alternatively, in years when snow cover is uniformly high, managers could plan to do less CLP control.

Previous authors have posited that the negative relationship between CLP and snow cover is driven by changes in under-ice light availability (Valley & Heiskary, 2012). Although the observed effect of winter snow depth on early-season CLP distribution supports this, our results from late surveys of untreated lakes (no significant effect of snow) indicate that factors other than winter conditions are stronger drivers of population dynamics as spring progresses. It is likely that spring water temperatures, which are known to strongly influence aquatic plant growth (Chambers et al., 1985; Woolf & Madsen, 2003), may be more influential on late-season CLP; however, springtime environmental conditions were not evaluated here.

Recent reviews of invasion biology have called for more research into anticipated interactions between climate change and invasive species (Buckley, 2008; Ricciardi et al., 2017). While much of this discussion revolves around the role that climate change plays in the risk of species movement or the establishment of those species (Seebens et al., 2015), critical questions remain about the influence that a changing climate will have on established invasive species' impacts and distributions, and the efficacy of management used to target them (Hellmann, Byers, Bierwagen, & Dukes, 2008). Climate change models indicate that recent trends of declining snowfall in Minnesota (except areas receiving lake-effect snow, which are outside of our study region) will continue (Pryor et al., 2014). Our results show that in years with less winter snow cover, CLP frequency increased. Thus, we expect that future distributions of CLP will increase as continuing climate change yields lower snow cover.

Environmental factors had little influence on CLP density, but strongly influenced its frequency. Because mean rake density is a metric that describes growth where the plants occur and frequency of occurrence describes the spatial extent of growth in a lake, the two metrics reflect differences in growth and occupancy of suitable habitat, respectively. Changes in frequency associated with changing environmental conditions are likely to be driven by decreases in plants residing in already marginal habitats, which would be unlikely to produce high densities under any conditions. For example, previous studies found low-light conditions limited growth of plants in deep water and that stem densities were highest in shallow waters (Tobiessen & Snow, 1984). This may also explain why herbicide treatments were less effective (relative to untreated lakes) in years of high snow depth. If plants persisting at low densities in marginal habitat were already eliminated by low winter light, managers might have focused efforts on higher-density areas in shallow habitats. Targeting of high-density stands may be reflected in diminishing reductions of frequency because such locations require very large decreases in biomass to fully transition from present to absent in a point–intercept survey (Valley & Heiskary, 2012). Finally, we have not considered spring growing temperatures in this study, but they are known to affect the density of other macrophytes (Rooney & Kalff, 2000). Our finding that density was not sensitive to the environmental factors we considered, but frequency was, suggests that these factors influenced the extent of suitable habitat, but not CLP performance within suitable habitat.

Although the scale of this dataset allowed us to discern broad-scale relationships, there was high variability in lake-level data. Additional variables outside the scope of our analysis influence CLP populations. Thus, even if managers account for the factors we found to be influential, treatments could fall short of expectations due to other factors. For example, spring conditions that are optimal for CLP growth could overwhelm effects of overwintering conditions. Additionally, this work has described the influence of environmental factors on CLP based on their relationships to one another in an observational dataset. To elucidate the mechanisms driving these influences, future work should explore the mechanisms posited here (e.g. snow limits distribution by altering light availability) through experiments enabling stronger causal inferences (Butsic, Lewis, Radeloff, Baumann, & Kuemmerle, 2017; Cunningham & Lindenmayer, 2017). Another limitation of these observational data is that, by definition, the lakes in this dataset drew the interest of managers—enough so that they felt it was necessary to conduct CLP-specific survey work and/or management. Thus, it is possible that our dataset could be biased towards lakes with more conspicuous (i.e. more abundant or nuisance-causing) CLP populations. However, summary statistics indicate good coverage of low-abundance populations, and the

dataset is geographically representative of known CLP populations in the state.

That our study only focused on one component of the outcomes of CLP management cannot be overemphasised. Although we have critically examined how CLP responded to management, other management objectives must also be considered, particularly responses of native plant communities to treatment (James et al., 2007; Jones et al., 2012). Such responses could include undesirable effects, such as negative impacts of herbicides on native plant communities (Kujawa et al., 2017), or diminished fish habitat where macrophyte communities are generally depauperate and CLP contributed vital structure (Kovalenko, Dibble, & Slade, 2010). Alternatively, reductions in CLP could release native macrophytes from competitive suppression, fostering recovery (Case, Harrison, & Cornell, 2016; Flory & Clay, 2009).

Researchers and managers should continue to work together to collate and analyse monitoring data to advance our understanding of invasive species ecology and management (Heger et al., 2013). Because of persistent uncertainty, we suggest that treatment regimens operate within the adaptive management cycle, with outcomes of management monitored and evaluated, and strategies updated accordingly (Buckley, 2008). Finally, it is vital to continue monitoring both managed and unmanaged lakes to enable stronger inferences about treatment effectiveness.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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