



Niche dynamics and potential distribution of *Butomus umbellatus* under current and future climate scenarios in North America

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Abstract Predicting the potential distribution of invaders is informative for pre-emptive policy or management decisions and identifying suitable areas for establishment of new populations. Temporal projection of potential distributions is complicated by the magnitude and pace of changing climate, which could alter suitability under future conditions. The wetland invader, *Butomus umbellatus* is widespread in the northern US and southern Canada, but potential for invasion into new areas is unknown. We used environmental niche modeling to address our hypotheses

for *B. umbellatus*: (1) a climatic niche shift has occurred between native and invasive ranges, (2) suitable areas in the invaded range have been colonized, and (3) climate suitability is likely to change in future climates. Environmental niche is highly conserved and stable (0.761) between ranges of *B. umbellatus*. Ensemble forecast revealed that nearly 60% of the invaded range is climatically suitable, including large areas in both the southern US and Alaska. Under future climates, there is a net decrease of suitable area, although two of three global circulation models predict range expansion of this species across gas emission scenarios. Given that the area is already invaded or at risk for future invasion, development of geographically adaptable long-term management strategies is prudent.

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Introduction

Understanding the potential distribution of a plant invader allows invasive species managers in at-risk areas to make informed decisions when allocating resources towards prevention, planning for future management activities, prioritizing management to most at-risk areas of negative impacts, or to include

the species in early detection and rapid response (EDRR) surveillance programs (Inglis et al., 2006; Hauser & McCarthy, 2009; Januchowski-Hartley et al., 2011). Mapping the potential distribution of a new invader may provide justification for investment into plant management research, particularly if the potential distribution of the invader is large with many uninvaded areas, and the risk of negative environmental impacts is great. Because species distributions are expected to shift with future climates (Parmesan & Yohe, 2003; Parmesan, 2006), an approach that includes future scenarios may provide additional justification for investing resources in management now and also provide a warning to water resource managers in areas currently at low risk of invasion.

The wetland weed, flowering rush [*Butomus umbellatus* (Linnaeus, 1753)], is native to Eurasia but has been introduced into the USA multiple times over the last 100 years (R Core Team, 1941) and is designated a ‘principal invasive alien’ (White et al., 1993). It now occurs in at least 14 states from Maine to Washington and four Canadian provinces (Gunderson et al., 2016; EDDMapS.org 2018). Infestations range in extent, but impacts caused by dense growth include degradation of wildlife habitat, impeded water flow, increased sedimentation, and increased incidence of cercarial dermatitis (swimmer’s itch) (Jacobs et al., 2011). In the USA, there are diploid and triploid cytotypes, and there are multiple genotypes (Gaskin in prep.) within cytotypes. Cytotypes are largely geographically separated, with triploid genotypes found primarily in the northwestern US and diploids in the upper midwestern and northeastern US. Management options are under investigation, and although there are no reliable widely used herbicide tools to control *B. umbellatus*, there have been promising results using diquat dibromide and endothall (dipotassium salt) in laboratory and growth chamber assays (Getsinger & Madsen, 2018) and diquat in field studies (Madsen, 2000). However, for various reasons, including restrictions because of concerns about non-target impacts on threatened or endangered species (e.g., salmonids in the Pacific Northwest), herbicides cannot be used in all areas. Under these circumstances, alternative management techniques are needed. A promising area of current research involves the development of host-specific insect or pathogen biological control agents of *B. umbellatus* found in the Eurasian native range.

In this context, understanding the potential distribution of *B. umbellatus* in its invasive range in North America under present and future climate conditions will be crucial for management implications. This information is necessary for prioritizing invasion hotspots, implementing EDRR for new invasions, and developing robust policy framework (Goncalves et al., 2014). Environmental niche models (ENMs) have been effectively used to identify areas within introduced areas that are climatically suitable for establishment and spread of invasive species (e.g., Mainali et al., 2015; Shrestha et al., 2018). ENMs operate by modeling statistical relationships between known occurrences of a focal species and environmental covariates, with an assumption that climatic niche of the species is conserved between its native and invasive ranges (Peterson et al., 1999). However, recent studies found evidence that species can undergo climatic niche shift during the process of invasion leading to increased uncertainty when identifying at-risk areas (e.g., Atwater et al., 2018).

This study was therefore conducted to identify (a) whether the climatic niche of *B. umbellatus* has been conserved between native and invasive ranges, (b) whether *B. umbellatus* has already colonized suitable areas in the invaded range, and (c) potential distribution of *B. umbellatus* under predicted climate change scenarios. To address these objectives, we first characterized the realized climate niche of the species in its native (Europe and parts of Asia) and invasive (US and Canada) ranges and then used an ensemble modeling framework to identify areas in its invasive range (primarily North America) that are currently, or may become, susceptible to the establishment of *B. umbellatus*. Given the long presence of the species in the USA, we expected that it already occupies most suitable areas in the invasive range. Additionally, following the trend of observed climatic niche shift for many invaders, we hypothesized that a realized climatic niche mismatch between native and invasive ranges of *B. umbellatus* would be detected and that under future climate scenarios the distribution of *B. umbellatus* would expand towards warmer areas of the southern US. However, there may be potential northward spread as well (Bradley et al., 2010), including into the state of Alaska.

Materials and methods

Generally, modeling activities in our study included two major steps: (i) data preparation and characterisation, (ii) modeling and projection, and (iii) Post-modeling analyses (Fig. 1). In the first step, niche and environmental characterization of collected *B. umbellatus* occurrence and climate data were conducted. A variety of niche modeling techniques were then used to project the potential distribution of *B. umbellatus* in North America.

Data preparation and characterisations

Collection of occurrence and climate data

Native (Eurasia) and invasive (US + Canada) occurrence records of *B. umbellatus* were collected from the Global Biodiversity Information Facility (GBIF) database using search terms '*Butomus umbellatus*' (GBIF.org (20 February 2019) <https://doi.org/10.15468/dl.qc8brl>). In addition to GBIF data, *B. umbellatus* occurrence in the invasive region also was accessed from EddMaps database (www.eddmaps.org).

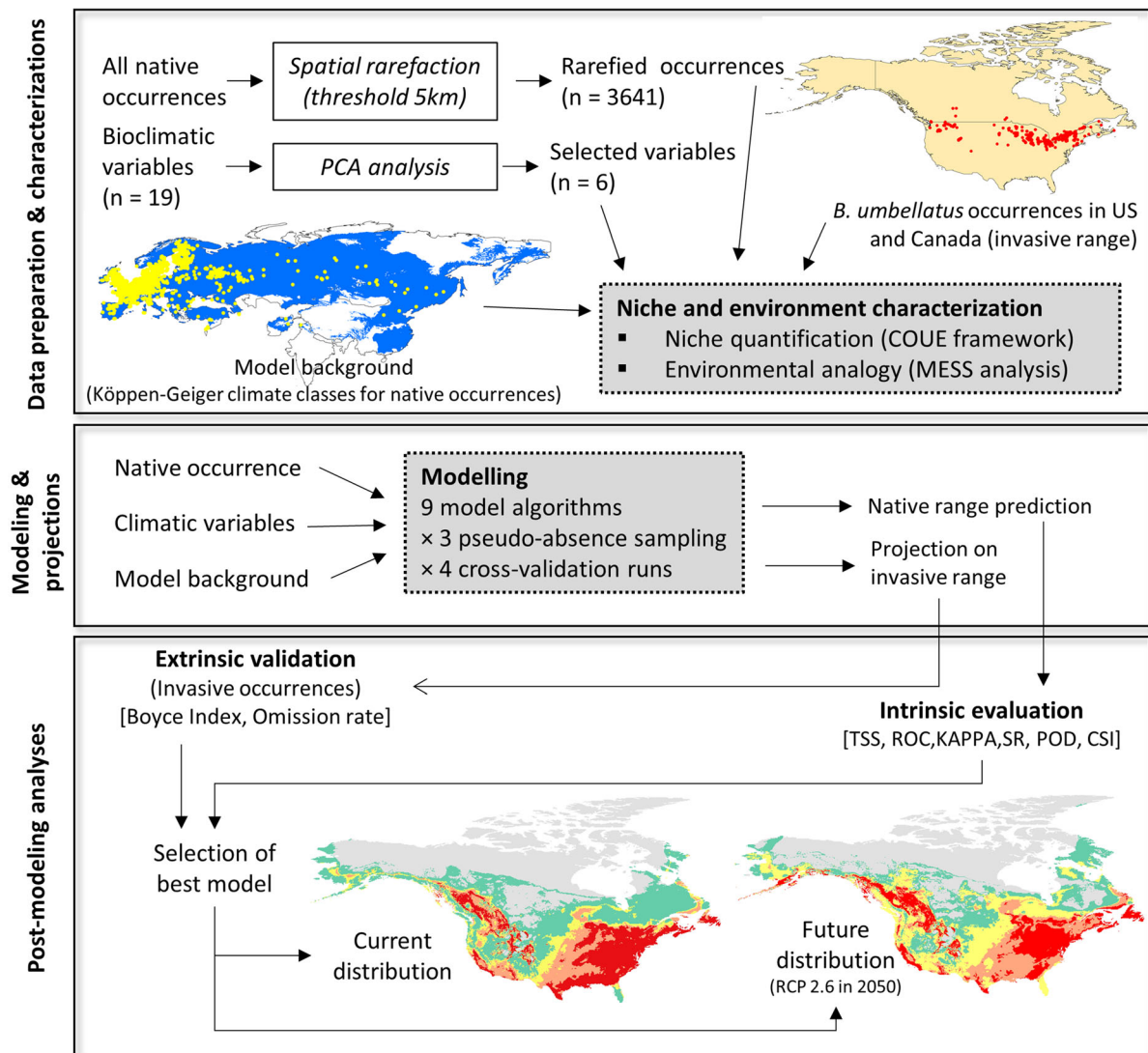


Fig. 1 General scheme of the modeling framework used in our study. Modeling activities involved three major steps: (i) data preparation and characterisation, and (ii) modeling and projection, and (iii) post-modeling analysis

org). Occurrence records were screened for duplicates. To avoid model overfitting and ensure validity of statistical analyses, occurrence records from the native range were spatially rarefied (using SDMtoolbox 2.3 in ArcMap 10.2.1) by selecting single point per grid cell (cell size = 10 km) (Brown, 2014). A total of 3641 occurrence records were kept for native range and 1,753 records for invasive range (see Online Resource 1).

We downloaded 19 bioclimatic variables from the WorldClim database version 1.4 (Hijmans et al., 2005), averaged over the 1950–2000 period, at a spatial resolution of 5 arc minutes (~ approximately 9 km resolution at the equator). To select the most important variables, we conducted a principal component analysis (PCA) using the ade4 package in R 3.5.3 (R 2017) and visualized the correlation between the variables. Six bioclimatic variables, namely, annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), temperature annual range (Bio7), annual precipitation (Bio12), precipitation of driest month (Bio14), and precipitation seasonality (Bio15), were selected based on their non-collinearity and contribution to overall environmental variation. For future climate projections, we used four IPCC greenhouse gas concentration pathways (i.e., representative concentration pathways; RCPs)—RCP 2.6, 4.5, 6.0, and 8.5, for two future periods—2050 and 2070. We chose three general circulation models (GCMs) of physical climate processes: the Beijing Climate Center Climate System Model [BCC_CSM1.1], the Community Climate System Model [CCSM4], and the Hadley Global Environment Model 2-Atmosphere Ocean [HAD-GEM2-AO]. The GCMs were selected based on the availability of predicted values of each of the bioclimatic variables and their reported performance in predicting the potential distribution of invasive species (e.g., Gillard et al., 2017; Manzoor et al., 2018; Ahmad et al., 2019).

Niche and environment characterization

Spatial transfer of the models from native to invasive ranges is uncertain if the available climate data is non-analogous between the two, both in univariate and multivariate space (Guisan et al., 2014). Therefore, prior to modeling, we quantified native and invasive niches using the centroid shift, overlap, unfilling, and

expansion (COUE) framework (Guisan et al., 2014) and assessed environmental analogy between two ranges using multivariate environmental similarity surface (MESS) (Elith et al., 2010) and the ExDet (Mesgaran et al., 2014) analyses.

Environmental niches of *B. umbellatus* in its native and invasive ranges were characterized by the first two axes of a Principal Component Analysis (PCA) conducted on the entire environmental space (i.e., chosen bioclimatic variables) of the two ranges. By applying a kernel density function, the occurrence points of both ranges were converted to smoothed densities of occurrences and plotted in the gridded environmental space. Observed niche overlap between native and invasive ranges was estimated using Schoener's index of niche breadth (D) and statistically evaluated using niche similarity test based on 95% confidence interval to test the null hypothesis of random expectation of niche similarity between native and invasive ranges (Broennimann et al., 2012). By overlapping environmental spaces of native and invasive ranges, we measured species niches by estimating unfilled niche of the native range (U), overlapping niche of both ranges (O), and expanded niche in the invaded range (E). These analyses were performed using the ecospat package version 3.0 (Broennimann et al., 2012) in R.

MESS analysis was computed using the package dismo (Hijmans et al., 2017) in R to compare the similarity of grid cells occupied by *B. umbellatus* in the invasive range with grid cells occupied by *B. umbellatus* in the native range, with respect to the set of selected bioclimatic variables. Grid cells with positive values were within the range of environmental values of the native niche, whereas grid cells with negative values indicated dissimilar environment for at least one variable (Broennimann et al., 2014). Furthermore, we used ExDet tool (Mesgaran et al., 2014) to identify two types of novelty between native and invasive ranges for the selected bioclimatic variables. Non-analogous environments were identified for individual covariates (i.e., outside the range of individual covariates of the native niche: type 1 novelty; NT1) as well as for novel combinations between covariates (i.e., within the univariate range of the native niche, but forming novel combinations between covariates in the invasive range: type 2 novelty; NT2).

Modeling and projection

To generate an ecologically meaningful model background, we first spatially intersected native occurrence points with the Köppen–Geiger climate layer (available from CliMond database, <https://www.climond.org/Koppen.aspx>) to identify currently occupied climate classes in Europe and Asia (Webber et al., 2011). We restrained the model background to include only those areas with previously identified climate classes. Following the BAM framework proposed by Barve et al. (2011), we considered the selected model background as the abiotically suitable area where the species could exist given unlimited dispersal.

We performed environmental niche modeling using nine different algorithms implemented in the biomod2 package (Thuiller et al., 2009) in R, including the following: three regression methods [GAM: general additive model (Hastie & Tibshirani, 1990), GLM: general linear model (McCullagh & Nelder, 1989), MARS: multivariate adaptive regression splines (Friedman, 1991)]; three machine learning methods [GBM: generalized boosting model (Ridgeway, 1999), MAX-ENT: Maximum Entropy (Phillips et al., 2006), RF: random forest (Breiman, 2001)], two classification methods [(CTA: classification tree analysis (Breiman, 1984), FDA: flexible discriminant analysis (Hastie et al., 1994)], and one envelope model [SRE: Surface Range Envelop (Busby, 1991)]. To meet the criteria of having absence (or pseudo-absence) data for most of these models (except SRE), we generated three equal-sized (to the true presence records) sets of random pseudo-absence (PA) points across the model background. The models were calibrated using 70% of randomly selected data. The other 30% of data were used for intrinsic model evaluation. The modeling process was replicated four times, thus generating a total of 108 models (9 algorithms \times 3 PA datasets \times 4 cross-validation runs).

Post-modeling analyses

Individual model performance was evaluated using six metrics—true skill statistic (TSS), the area under the curve of receiver operating characteristics (ROC), Cohen's Kappa (KAPPA), Success Ratio (SR), Probability of detection (POD), and Critical Success Index (CSI), as implemented in the biomod2 package. In addition to intrinsic evaluation using the test data

(native occurrence) from resampling procedure, we assessed model performance using the independent invasive occurrence data (external evaluation) following the recommendation of Guisan et al. (2017). Models with high predictive accuracy (TSS > 0.7; ROC, SR, POD, CSI > 0.8; KAPPA > 0.5) were used for projection in the invasive range. Individual projection was validated for invasive range occurrences using two metrics—omission rate (OR = proportion of test points falling in pixels not predicted suitable) and Boyce index (BI). Threshold-independent BI ranges from -1 to 1 and provides an assessment of the degree to which model predictions differ from random expectation (Boyce et al., 2002). A positive BI value indicates predictions consistent with the evaluation dataset, values near zero indicate random predictions, and negative values indicate incorrect predictions (Boyce et al., 2002). In this study, we used the ecospat package in R to estimate the modified BI following Hirzel et al. (2006). Models having positive BI value and lowest OR were used to build an ensemble model with a weighted mean approach.

We used the ensemble forecast method of the biomod2 package to map the potential distribution of *B. umbellatus* in North America, under both current and future climate scenarios. Minimum presence values (MPV) obtained by invasive occurrence data were used as cutoffs to eliminate pixels unsuitable for *B. umbellatus* growth (binary predictions). Using pixels with values above MPV, classified suitability maps were generated based on omission percentage of occurrence points: 10% omission (low suitability), 10–25% omission (mid low suitability), 25–50% (mid high suitability), and > 50% (high suitability). Raster overlay analysis was conducted with binary predictions from three GCMs and a combined raster was produced based on prediction analogy. The combined raster was then overlain with the current binary prediction to identify range change. ArcMap 10.2.1 was used to perform all these analyses and visualize the outputs.

Results

Niche conservatism and environmental analogy

The first two PCA axes explained maximum environmental variation between native and invasive ranges

(69.47%) (Fig. 2a). The three variables that contributed most in explaining variation in native occurrence data were minimum temperature of the coldest month (bio06), mean temperature of coldest quarter (bio11), and temperature annual range (bio07) (Table 1). The hypothesis of the retained niche similarity was rejected ($P = 0.039$) indicating that realized climatic niches in the invasive range were more similar to that of the native range than would be expected at random. Low degree of niche overlap ($D = 0.255$) (Rödder & Engler, 2011) was observed between native and invasive ranges. High niche stability (0.761) along with low expansion (0.239) and unfilling (0.131) indicate that *B. umbellatus* has occupied most of its native niche in its invasive range (Fig. 2b).

The MESS analysis revealed that a large part of the invasive range of *B. umbellatus* is climatically similar to the native range (positive values) which is in accordance with the distribution of the invasive occurrences (Fig. 3a). From the ExDet map, it is evident that the majority of the invasive range is within the univariate range of climate covariates of the native niche (green in Fig. 3b), whereas the NT1 component (type 1 novelty, marked red in Fig. 3b) is restricted to the northern part of the invasive range. These findings are indicative of model transferability in geographic space, i.e., the potential distribution of

the species in the invasive range generated using native occurrences and selected bioclimatic variables can be interpreted with confidence.

Model evaluations

The intrinsic model evaluation (Fig. 4a; Online Resource 2) revealed that all the individual modeling algorithms had high predictive accuracy with RF to be the most accurate on average (5 out of 6 metrics). Therefore, all models were used to forecast the potential distribution of the species in its invasive range. Extrinsic evaluation of these forecast outputs with the invasive occurrence data revealed positive BI values for 4 modeling algorithms—FDA, MAXENT, Phillips, RF, and SRE (Fig. 4b), among which lowest OR was observed for the RF algorithm (0.00084 ± 0.0003). Therefore, the models generated using the RF algorithm ($n = 12$ for 3 PA datasets \times 4 cross-validation runs) were used to build the ensemble model and included in the ensemble forecast.

Potential distribution

Based on potential distribution maps, 56.9% of the entire invasive range in North America is climatically suitable for *B. umbellatus* distribution under current climatic conditions (Fig. 5). In the USA, eastern and

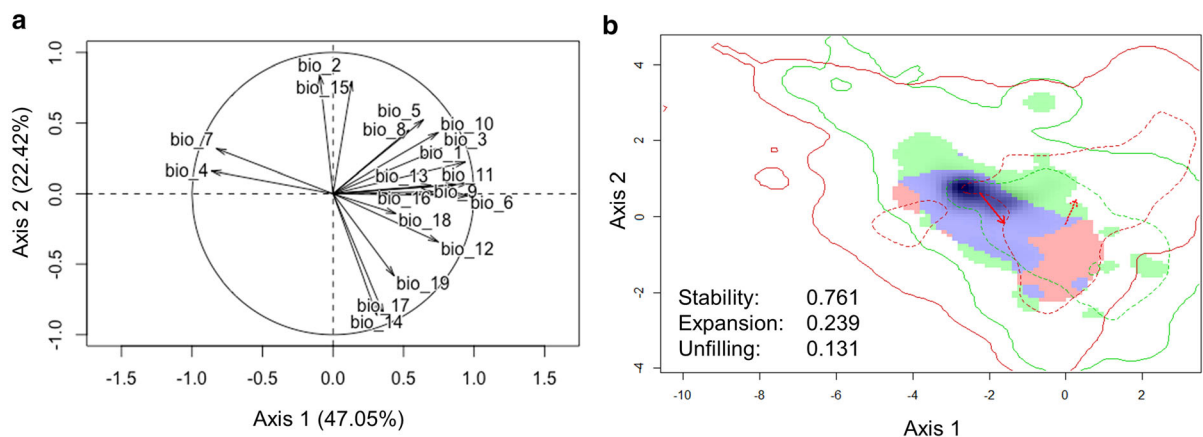


Fig. 2 Characterization of climatic niches of *B. umbellatus* in its native and invasive ranges—(a) the correlation circle describes the importance of each of the 19 bioclimatic variables along the two PCA axes; (b) visualization and quantification of climatic niches (COUE framework) based on the selected bioclimatic variables—contour lines delineate the available niche in its native range (green) and in invasive range (red). The solid

lines represent 100% available environment, whereas the dotted lines represent 50% of the same. The green colored areas correspond to the unfilled zone of the native niche (U), blue areas represent the overlap zone of the two niches (O), and the red areas delineate the expansion zone in the invasive range (E); red arrows represent how the center of the niche has changed between native and invasive ranges (C)

Table 1 Loadings on two PCA axes of bioclimatic variables

Variables	Description	Axis 1 (47.05%)	Axis 2 (22.42%)
Bio1	Annual mean temperature	0.878	0.363
Bio2	Mean diurnal range	− 0.497	0.651
Bio3	Isothermality	0.658	0.296
Bio4	Temperature seasonality	− 0.914	0.118
Bio5	Max temperature of warmest month	0.379	0.685
Bio6	Min temperature of coldest month	0.952	0.074
Bio7	Temperature annual range	− 0.916	0.203
Bio8	Mean temperature of wettest quarter	0.152	0.572
Bio9	Mean temperature of driest quarter	0.837	0.091
Bio10	Mean temperature of warmest quarter	0.565	0.641
Bio11	Mean temperature of coldest quarter	0.942	0.154
Bio12	Annual precipitation	0.768	− 0.053
Bio13	Precipitation of wettest month	0.509	0.415
Bio14	Precipitation of driest month	0.695	− 0.578
Bio15	Precipitation seasonality	− 0.347	0.739
Bio16	Precipitation of wettest quarter	0.552	0.337
Bio17	Precipitation of driest quarter	0.720	− 0.554
Bio18	Precipitation of warmest quarter	0.322	0.327
Bio19	Precipitation of coldest quarter	0.756	− 0.399

Values > 0 indicate a positive contribution, whereas those < 0 indicate a negative contribution to the axis

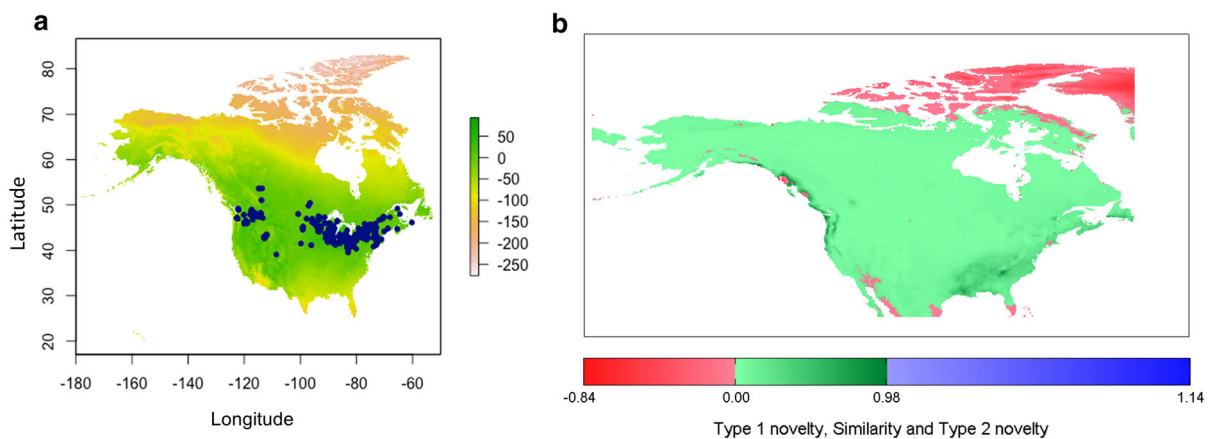


Fig. 3 Quantification of environmental analogy between native and invasive ranges of *B. umbellatus*—(a) the multivariate environmental similarity surface (MESS) map; dark green areas (positive MESS values) correspond to sites in the invasive range with similar climatic conditions to the native range; the yellow-to-light red gradient (negative MESS values) indicates the degree of dissimilarity in the invasive range with the climate of the native distribution; (b) the ExDet map of the extrapolated

projection areas; green colored areas indicate similar climatic condition between native (reference data) and invasive (projection space) ranges; the Type 1 novelty (red) indicates areas in the invasive range (projection space) with at least one bioclimatic variable outside the univariate range of the native range (reference data); the type 2 novelty (green) indicates areas with non-analogous bioclimatic variable combinations that have not been found in the invasive range

southeastern states were found to be highly suitable. Low-to-moderate suitability was projected in southern Alaska. Climatic suitability is lower in the central US,

whereas low-to-moderate climatic suitability was observed for the western and southwestern US. In Canada, southern and southeastern areas are

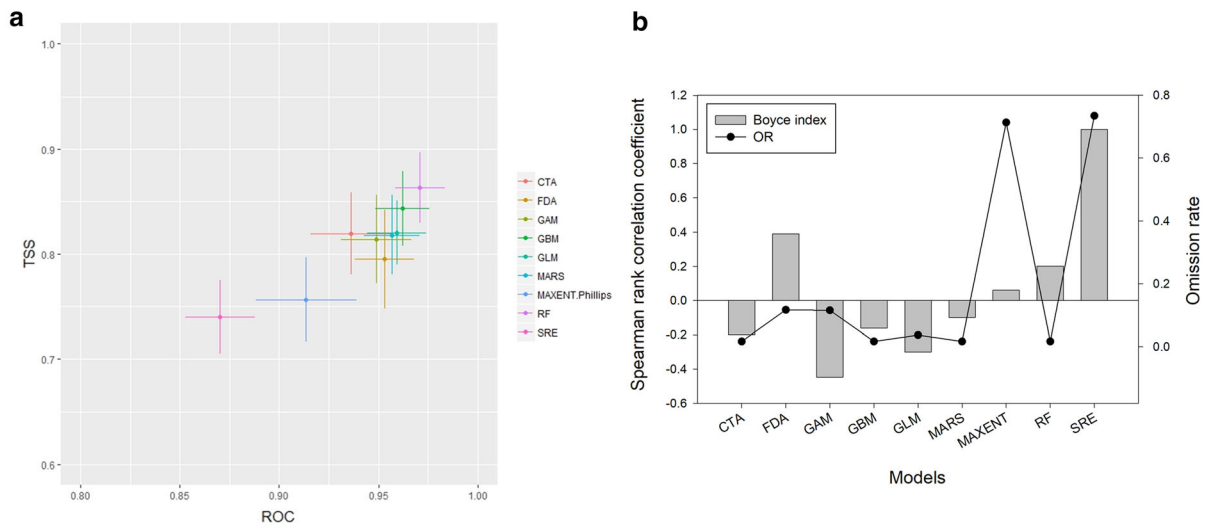


Fig. 4 Intrinsic and extrinsic evaluation of model performance—(a) mean model evaluation scores according to two evaluation metrics [ROC (AUC) and TSS] estimated using test

data of native occurrence (intrinsic evaluation); (b) mean omission rate (OR) and Boyce index values estimated using invasive occurrence data (extrinsic validation)

moderately suitable for *B. umbellatus*. The majority of the Canadian landmass was found to be climatically unsuitable for *B. umbellatus* (Fig. 5).

Under future climate conditions, the potential invasive distribution of *B. umbellatus* is predicted to decrease across 6 of 8 future gas emission scenarios

considered in this study (Fig. 6). A maximum decrease in climatically suitable areas is predicted in low gas emission scenarios in 2050 under RCP 2.6 (10.2%) and in 2070 under RCP 4.5 (10.1%) (Table 2). Certain areas of the northern and midwestern US (states of Montana and Wyoming), and southern and eastern

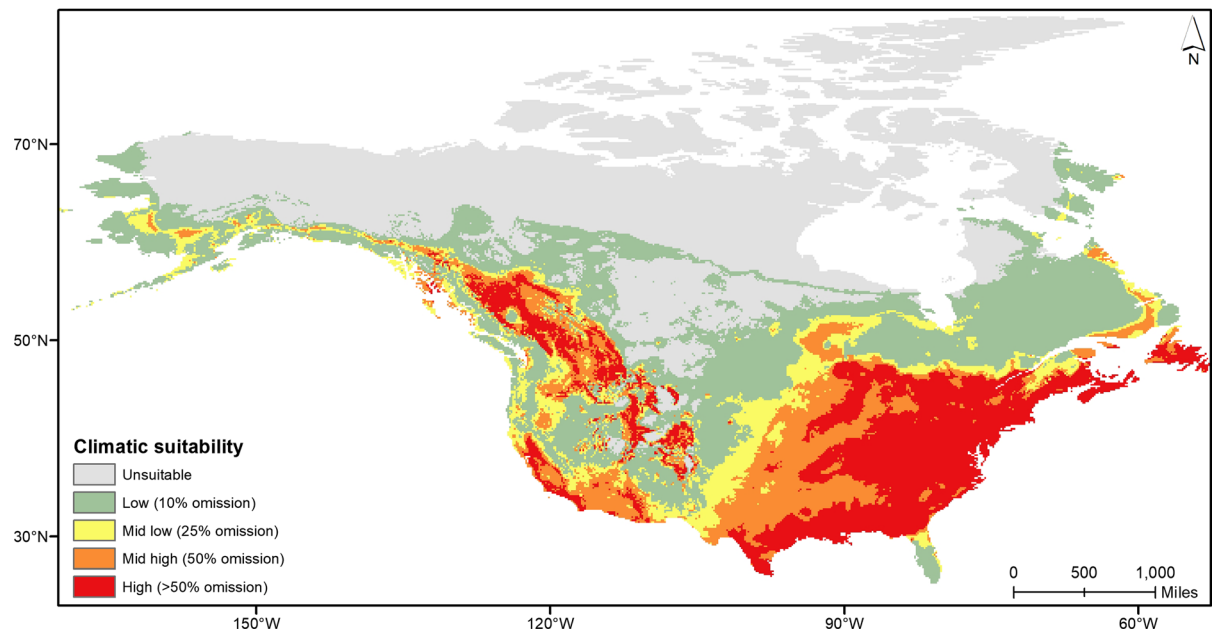


Fig. 5 Potential distribution of *B. umbellatus* in the US and Canada under current climate conditions; legends depict five climate suitability classes based on thresholds calculated in terms of minimum training presence of known occurrences

Canada (Saskatchewan, Alberta and Quebec) are predicted to become climatically unsuitable for *B. umbellatus* (Fig. 6). An increase in climatically suitable areas was observed only in 2070 under RCP 6.0 (8.8%) and in 2050 under RCP 8.5 (1.3%). In the USA, western parts of Alaska, the southern provinces of Canada, western Quebec, and parts of Northwest Territories are predicted to become more suitable under high gas emission scenarios. Analyzing the three GCMs separately, we found considerable variation in the predicted range change across the models (Table 2; Online Resource 3). Differences between areas predicted to become suitable (gain) or unsuitable (loss) under 8 possible future climate scenarios (4 RCPs \times 2 time periods) revealed loss > gain in 5 scenarios under the CCSM4, whereas loss < gain was observed in all scenarios under the BCC_CSM1.1 and HADGEM2-AO (Table 2).

Discussion

In this study, we predicted current and future distributions of *B. umbellatus*, an aggressive colonizer of shallow water habitats in North America. The findings, being the first for this invasive species, have important management implications.

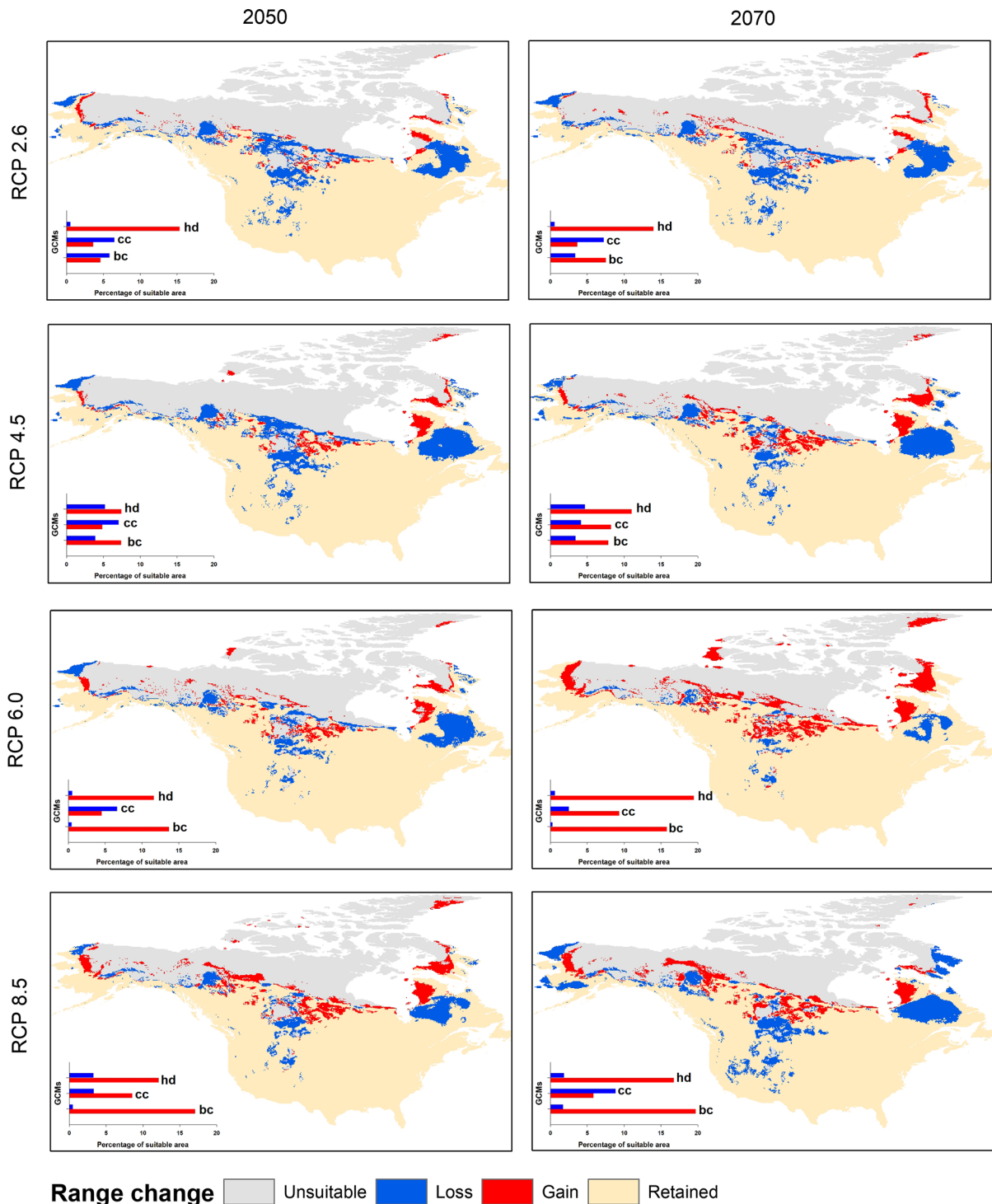
Current and potential distribution

With respect to bioclimatic variables, our study revealed that variables related to cold temperature (bio6, bio11 and bio7) made significant contributions in governing the distribution of this species overall. Unsurprisingly, the current invasive distribution of *B. umbellatus* is the northern tier of the USA and Southern Canada, but there is clear potential for southward spread (Fig. 5), especially since populations are already established in the Mississippi River. Multivariate analysis of realized climatic niche requirements revealed moderate overlap between its native and invasive ranges, suggesting that the species has adapted to unique environmental conditions encountered in its invasive range. Niche stability less than one (0.761) indicates that *B. umbellatus* may have undergone a shift in its realized climatic niche, a phenomenon frequently reported for invasive species (; Broennimann et al., 2007; Elith et al., 2010; Atwater et al., 2018), including other aquatic invaders (Escobar

et al., 2016; Ribas et al., 2018). For example, the observed environmental niches of the aquatic invader *Hydrilla verticillata* [(L.f.) Royle, 1839] in South and North America are thought to be the subsets of its native range niche, likely a consequence of founder effects during invasion (Ribas et al., 2018). In the case of *B. umbellatus*, mismatch between realized climatic niches may be a consequence of niche expansion (in comparison to niche unfilling) towards warmer areas of the southern US (Fig. 2b). This distribution pattern may be explained by the broad thermal tolerance of the species, producing a high probability of establishing in differing climates (Centre for Invasive Species and Ecosystem Health, 2010; <https://www.invasive.org/browse/subinfo.cfm?sub=5219>), due to the lack of interspecific competition with ecologically similar species (Mott, 2010) or lack of natural enemies in the warm environment of the southern US (e.g., the European semi-aquatic weevil *Bagous nodulosus* Gyllenhal, 1836).

Areas in the southern US are climatically suitable for flowering rush establishment (Fig. 1); however, until recently, flowering rush was not reported south of N40° and it has been unclear what factors most limit southward spread in the USA. Interactions with other species, such as predation or disease, may be important in limiting the southern distribution of flowering rush in the USA. Harms et al. (2019) found latitudinal gradients in disease affecting a triploid flowering rush genotype in the USA, but not a diploid genotype, suggesting that pathogenic organisms could play a role in defining the southern range limits of triploid plants in the USA. Other factors like limited propagule pressure, genetic differences between plants in the introduced and native ranges (i.e., post-introduction genetic drift or adaptation), or genetic bottlenecks experienced during introduction may also lead to the distribution pattern observed in the USA (Suzuki-Ohno et al., 2017).

This study led to the prediction that there will be a decrease in suitable *B. umbellatus* habitats in its invasive range under future climate change scenarios, and this is in accordance with the predictions of other macrophyte species (Gillard et al., 2017). However, the influence of individual GCMs on this range prediction is noteworthy. Indeed, the cool leading edge of the range is predicted to shift northwards towards Alaska in and southern provinces of Canada for two GCMs considered in our study. These findings



provide support to the growing evidence that the GCM used can contribute to variation in model predictions of a species' range dynamics under future climate

scenarios (Diniz-Filho et al., 2009; Peterson et al., 2018). Northern range expansion is not surprising for *B. umbellatus* since a prominent role of cold winter

Fig. 6 Overlay maps of binary projections of *B. umbellatus* in the US and Canada showing changes in the potential distributions (loss and gain with respect to current climate condition) across four representative concentration pathways (RCPs) by 2050 (left column) and 2070 (right column). The inset bar plots indicate percentage of change (loss and gain) in the number of suitable pixels with respect to current climate condition for three individual global circulation models (GCMs): bc = Beijing Climate Center Climate System Model; cc = Community Climate System Model; hd = Hadley Global Environment Model 2-Atmosphere Ocean

stratification on seed germination and survivability has been documented (Hroudová & Zákavský, 2003). Similar range expansion has been documented for other macrophyte species under predicted and observed climate change (Rahel & Olden, 2008; Alahuhta et al., 2011; Bellard et al., 2013). For example, threadleaf water-crowfoot [*Ranunculus trichophyllus* (Chaix & Dominique, 1786)] was recently documented to establish in high-elevation locations that would have been historically protected from *R. trichophyllus* due to extended ice cover during winter months. Due to warming conditions, the period of ice cover has been reduced, allowing establishment (Lacoul & Freedman, 2006). Although we did not have the ability to model at the spatial resolution to make fine-scale predictions about habitat suitability, it is worth highlighting that only water bodies and other wet areas within these climate matched regions are at risk, particularly in shallow areas of both lentic and lotic systems.

Our predictions about range dynamics are based on an assumption of limited adaptation to the climates experienced in the contracting range margins. In general, climate matching to predict future species distributions relies on the assumption of zero evolutionary capacity for adaptation to new climates, but this is probably false for most species (Hancock et al., 2011; Hällfors et al., 2016). In addition to genetic adaptation, phenotypic plasticity of key functional traits influence a species' response to new environments, such as those that might be encountered during climatic change (Diniz-Filho et al., 2019). Finally, the timescale at which climate change occurs is critical, particularly for dispersal-limited organisms' ability to track suitable climate into new geographic areas (Angert, 2009; Hargreaves et al., 2015). For flowering rush, a species with limited genetic diversity and

predominantly clonal propagation in the USA (Fernando & Cass, 1996), it is unclear whether local adaptation to climate is important in defining its current US distribution or what role it will play in its future distribution. Phenotypic plasticity in functional traits along habitat gradients (e.g., water depth) in North America has been reported for *B. umbellatus* (Carter et al., 2018). Given the observed expansion of the realized climatic niche in its invasive range, it is likely that phenotypic plasticity is important to the adaptive potential of the species in novel environments (and future climates). In this context, the potential distribution of the species under current and future climates generated from our study should be supplemented with experimental investigations into plant tolerance and performance across environmental gradient to better define potential for spread in North America.

Implications for management

After introduction in 1905 near Montreal along the St. Lawrence River (Core, 1941), the popularity of *B. umbellatus* as a water garden ornamental and its subsequent escape into natural areas have promoted spread in North America. Given that the species is still actively sold in the US market (Funnell et al., 2009), and the abundance of vegetative propagules that can be produced by a single plant (Lui et al., 2005), range expansion is expected. Since long-term management of *B. umbellatus* infestations can be complex and costly (Turnage et al., 2019), early detection is crucial to prevent its establishment, spread, and negative impact in new areas (Leuven et al., 2017). In this context, the assessment of climatic suitability in North American locations in order to support decision-making related to management appears to be justified. Successful management of invasive species often depends on accurate identification of the current and future suitable habitats. Our findings provide baseline data for implementing management strategies at a relatively early stage of invasion and quarantine measures to protect unimpacted regions from future *B. umbellatus* invasion. We found that although the current distribution of flowering rush in the US and Canada is large, there is potential for it to be much larger, both now and in the future. Of particular note is that although not yet recorded in Alaska, water resource managers there should be aware of this

Current	GCMs	RCPs							
		2.6		4.5		6.0		8.5	
		2050	2070	2050	2070	2050	2070	2050	2070
61441	Combined	55425 (− 9.79%)	55164 (− 10.22%)	55236 (− 10.09%)	58221 (− 5.24%)	58288 (− 5.13%)	66872 (8.84%)	62188 (1.22%)	57344 (− 6.67%)
	BCC_CSM1.1	60189 (− 2.04%)	65669 (+ 6.88%)	64928 (+ 5.68%)	65964 (+ 7.36%)	74771 (+ 21.70%)	77098 (+ 25.48%)	78206 (+ 27.28%)	79573 (+ 29.51%)
	CCSM4	42339 (− 31.09%)	57831 (− 5.88%)	59195 (− 3.66%)	65532 (+ 6.66%)	59311 (− 3.47%)	68339 (+ 11.23%)	66686 (+ 8.54%)	58371 (− 4.99%)
	HADGEM2-AO	76413 (+ 24.37%)	74971 (+ 22.02%)	63724 (+ 3.72%)	67847 (+ 10.43%)	72633 (+ 18.22%)	80436 (+ 30.92%)	70404 (+ 14.59%)	76450 (+ 24.43%)

species since nearly 48% of Alaska has been found to be climatically suitable for this species. Given that Alaska has a large proportion of US wetlands (Hall et al., 1994), monitoring of lakes and wetlands around ports of entry should remain vigilant. Similar management approaches based on identifying climatically suitable habitat has been undertaken for other aquatic invasive plant species in North America (Koncki & Aronson, 2015).

Other factors related to spread of flowering rush should also be investigated to better refine predictions of establishment risk. For example, most ENMs make predictions about species' ranges without genetic information beyond species identity and are limited to examination of the more easily identifiable species-level distribution despite evidence of genotypic variation in distribution-limiting factors for some species (Zhu et al., 2017; Williams et al., 2018). In the case of *B. umbellatus* invasion in North America, there exists geographic population structure, with diploid and triploid plants found predominantly in different parts of North America (east and west, respectively). In a morphological analysis, Anderson et al. (1974) suggested that plants from the Great Lakes and western North America (likely the triploid) were from Europe, while plants from the St. Lawrence River region (likely the diploid) were more similar to those from Asia. Additionally, the diploid and triploid forms differ in reproductive strategy as well as the vectors and pathways of invasion (Eckert et al., 2000; Lui et al., 2005). These disparate geographic distribution patterns of cytotypes and their specific climate tolerances may influence their potential distributions and consequently may be important for cytotype-specific management. A limitation to our study is that low genetic resolution is available for *B. umbellatus* populations in its native range, including for genotypes introduced in the USA. For example, Klüber & Eckert (2005) found that the North American triploid genotype is most genetically similar to plants from the Netherlands and northern Germany, but at this point, we do not have genetic information from the Asian portion of the native range. Therefore, the location information used in the current study to match climates between native and introduced areas lacks the genetic resolution to make genotype or cytotype-specific inferences on current or future distributions.

In addition to the role of predictive niche modeling to support EDRR for effective management of new but

important invaders, climate suitability and similarity between native and invasive ranges play a role in the development and implementation of biological control (i.e., the intentional introduction of host-specific natural enemies to reduce target species abundance below threshold damage levels; (Van Driesche et al., 2009). Climatic mismatches between agent native and introduced ranges can lead to spatial heterogeneity in control success once the agent is introduced for weed control. For example, the giant salvinia weevil, *Cyrtobagous salviniae* Calder & Sands, 1985 is only effective at controlling *Salvinia molesta* [D. Mitch., 1972] (giant salvinia) in warm areas within the southeastern US, despite the distribution of its host plant which includes some temperate areas (Mukherjee et al., 2014). This lack of control in cooler areas has led to further native range surveys in regions that are better climate-matched with the temperate range of giant salvinia in the USA in order to find cool-adapted biotypes of *C. salviniae* (Russell et al., 2017). Given that the biological control of *B. umbellatus* is under development (Hafliger et al., 2017; Harms et al., 2019), it may be valuable to take into account both its current and potential future distributions in the invaded range when sourcing agents to ensure that they are pre-adapted to climates where they will ultimately be introduced (Sun et al., 2017).

Given the worldwide distribution of *B. umbellatus* (outside the US and Canada), there is strong potential for establishment in parts of the study area where *B. umbellatus* does not currently exist. However, it is unknown whether genotype identity of North American populations will be important in determining future spread and establishment in introduced areas. Genetically based variation in response to management tools such as herbicides and highly host-specific biological control agents has been documented in weed systems (Maxwell et al., 1990; Jasieniuk et al., 1996; Gaskin et al., 2011), and we propose that such variation be examined in the case of flowering rush. Future explorations in the native range of flowering rush should also focus on characterizing genetic information with the goal of increasing resolution and improving the risk assessment of spread and establishment in its invasive range.

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