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Model-based scenario planning to develop climate change adaptation strategies for rare plant populations in grassland reserves

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ABSTRACT

Incorporating climate change into conservation decision-making at site and population scales is challenging due to uncertainties associated with localized climate change impacts and population responses to multiple interacting impacts and adaptation strategies. We explore the use of spatially explicit population models to facilitate scenario analysis, a conservation planning approach for situations of high uncertainty. We developed dynamic, linked habitat suitability and metapopulation models using RAMAS GIS to consider management and monitoring options for a grassland reserve in Minnesota (USA) in order to support a hydrologically sensitive rare orchid (*Cypripedium candidum*). We evaluated 54 future scenarios combining changes in drought frequency, increased depth to water table, and multiple configurations of increased invasive species cover and management. Simulation results allowed us to prioritize adaptation strategies and monitoring guidelines to inform adaptive management for our model system. For example, preventing further spread of invasive species into the current *C. candidum* population is an important low-risk resilience strategy for this site. However, under more serious climate change scenarios, higher-risk strategies, such as protecting critical recharge areas, become essential. Additionally, allocating limited monitoring resources toward detecting changes in depth to water table and assessing *C. candidum* population responses to severe drought will more efficiently inform decisions about when to shift from low-risk resilience approaches to higher-risk resistance and facilitation strategies. Applying this scenario-based modeling approach to other high-priority populations will enable conservation decision-makers to develop sound, cost-effective, site-specific management and monitoring protocols despite the uncertainties of climate change.

1. Introduction

Climate change adaptation is an increasingly important component of conservation decision-making at multiple scales. Recently, adaptation has gained traction in conservation planning at national and regional scales (IPCC, 2014; Stein et al., 2013) in response to readily observed impacts, recognition of the inevitability of climate change regardless of mitigation efforts (Meehl et al., 2006), and growing awareness that existing reserves may fail to sustain vulnerable populations and plant communities into the future (Monzón et al., 2011). However, a significant gap remains between incorporating adaptation strategies into regional- and agency-level planning versus site-specific decision-making and implementation (Bierbaum et al., 2013). This gap is problematic because much of conservation decision-making necessarily occurs at the scale of individual sites and populations, whether it be land acquisition to protect and buffer conservation areas, vegetation management plans that address local threats, or monitoring programs to assess population viability and the need for possible rescue strategies (Loss et al., 2011; McLachlan et al., 2007). Research that increases understanding of how climate change impacts manifest at the site and population level is therefore important for facilitating conservation decision-making and prioritizing adaptation strategies across the full range of critical scales.

Greater availability of informational tools, resources, and frameworks for decision-making has helped overcome some of the previous barriers to incorporating climate change into conservation policy and practice. Downscaled climate projections and associated vulnerability assessments effectively inform regional planning by identifying risks to species and ecosystems (Galatowitsch et al., 2009; Groves et al., 2012; Hole et al., 2011; Williams et al., 2008). Additionally, decision-making frameworks such as scenario planning and structured decision-making can facilitate conservation planning in the face of uncertainty (Ogden and Innes, 2009; Peterson et al., 2003). However, incorporating climate change information into site-scale planning and management remains somewhat superficial, due – in part – to several key knowledge gaps: What localized impacts may result from the interaction of regional climate change with site features? What are the likely net effects of multiple interacting climate change impacts experienced by a given site or population? What adaptation strategies are likely to

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be most effective for a given site or population? And how (and when) can specific populations be expected to respond to climate change impacts and adaptation actions?

The question of localized climate change impacts has, thus far, received relatively little attention beyond the rather coarse bioclimatic envelope approach which can be used to explore potential ecological outcomes of regional climate change through comparison to a geographic analog (e.g. Galatowitsch et al., 2009, Hole et al., 2011). Truly localized impacts will result from the interaction between regional climate change and site features, such as topography, hydrology, and species composition. For example, regional climate change projections may indicate higher temperature and more variable precipitation, but resulting changes in soil water availability will depend on local features, including soil texture and drainage class, vegetative cover, topography and resulting hydrology (e.g. areas of recharge vs. discharge). Thus, on a site scale, climate change impacts may not manifest uniformly, and areas of currently suitable habitat for a given species may vary in their vulnerability to climate change. The ability to predict the most pressing local impacts, as well as identify both vulnerable habitat and potential on-site refuges, would not only enable more targeted management, but could also inform decisions about when – and where – to apply resistance, resilience or facilitation strategies (Galatowitsch et al., 2009).

Additionally, a given site or population will inevitably be affected by multiple climate change impacts, including chronic, long-term trends (e.g. increasing mean temperatures), changing frequencies in extreme climatic events (e.g. floods and drought; Easterling et al., 2000), as well as indirect effects of climate change (e.g. increasing rates of invasion by non-native species; Bradley et al., 2010; Diez et al., 2012). Effects of climatic "events" versus trends and indirect effects mediated through biotic interactions are particularly difficult to predict with precision (Jentsch et al., 2007; Staudinger et al., 2013), yet failing to account for these effects will yield an overly narrow – and likely overly optimistic – range of potential future scenarios. Simply understanding the response of species and communities to a single climate change parameter in isolation of others is likely insufficient, as combinations of impacts may either exacerbate (Bradley et al., 2010; Staudt et al., 2013; Zedler, 2009) or mitigate (Wyckoff and Bowers, 2010) the realized effects. Lacking data on such interactions, it can be difficult to prioritize which potential impacts to address. Managers may opt to focus on impacts they perceive to have the greatest certainty (e.g. model agreement on increasing temperatures), or simply continue existing "low-risk" resilience strategies. While these are not inherently unreasonable approaches, a failure to address the most damaging of impacts or to account for exacerbating interactions may lead to costly inefficiencies and a failure to sustain targeted populations (Staudt et al., 2013).

These knowledge gaps pose the greatest risk to conservation of rare and endangered species because their inherent vulnerability contributes to a greater risk of population decline in response to climate change and leaves little room for error in decision-making. Fine-resolution spatial variability in climate change impacts will be particularly important to rare and endangered plant species, which may occur in only a single location within a site and lack the capacity to disperse into future habitat refuges. Moreover, when the risk of extinction is already so high, precise estimates of sensitivities to interacting climate change impacts–– and management strategies – become critical. Unfortunately, while the pressing need for data on species' responses to climate change is well recognized (Staudinger et al., 2013), opportunities to experimentally test responses of rare and endangered species are quite limited. Difficult decisions, such as when to abandon conservative approaches (e.g. resilience strategies) in favor of high-risk, high-reward strategies like assisted migration, must therefore be made with little guiding information.

Models that incorporate high-resolution spatial data and multiple climate change impacts can play an important role in informing management decisions at the site and population scale by allowing us to explore population responses under multiple future scenarios, identify the most important impacts and interactions between multiple impacts, and make decisions about when to shift between different management strategies (e.g. resistance, resilience, and facilitation approaches). Others have effectively applied similar modeling approaches to conservation and restoration planning at broader regional scales (Bonebrake et al., 2014; Conlisk et al., 2014; Franklin et al., 2014; Lawrence et al., 2014), but applying this approach to the site-scale allows for an even greater degree of specificity, making it a valuable tool for informing and accelerating adaptive management. Richer model output resulting from more nuanced and high-resolution model scenarios could inform planning and evaluation stages of adaptive management by facilitating the prioritization of management strategies, focusing monitoring efforts, and allowing for earlier detection of responses to climate change and management, which may be especially critical for sustaining rare, endangered, and highly vulnerable populations. In turn, monitoring results can be used to refine model parameters and scenarios, resulting in increasing accuracy and relevance with future cycles of adaptive management.

Our objective for this research was to develop a model that incorporated interactions between multiple climate change impacts, management strategies, and site features in order to inform conservation management at the site scale. To this end, we developed dynamic, spatially-explicit, linked habitat suitability and metapopulation models (Akçakaya, 2000; Keith et al., 2008) for a rare orchid species of wet grasslands and fens, incorporating species population biology, fine-resolution spatial data, and future scenarios based on combinations of regional projected climate change impacts and invasion management outcomes. We aimed to directly inform adaptation strategies and monitoring protocols for vulnerable plant species of wet grasslands, while also investigating more broadly the importance of considering multiple impacts and site features in climate change impact studies.

Our model species, *Cypripedium candidum* Muhl. ex Willd. (small white lady's slipper), is a rare orchid occurring in wet prairies, meadows, and calcareous fens of eastern North America (Bowles, 1983). Populations have declined dramatically in response to wide-scale habitat loss and conversion, and it is currently listed as globally vulnerable by the IUCN Red List (Rankou, 2014), federally endangered in Canada (Species at Risk Act, 2002) and as endangered, threatened, rare or extirpated in most U.S. states within its range (Bowles, 1983; USDA NRCS, 2014a). *C. candidum* is potentially a high risk species with respect to climate change, as its wet prairie habitat and required hydrologic conditions are considered vulnerable to regional climate change impacts such as water table drawdowns and increased frequency of severe drought (Galatowitsch et al., 2009). Although its ability to withstand environmental stress via dormancy may provide some buffer against the effects of climate change (Shefferson et al., 2005), *C. candidum* is long-lived, slow to mature, and has low recruitment—species' traits that increase its likely vulnerability (Staudinger et al., 2013). Furthermore, because *C. candidum* tends to occur in isolated populations within a highly fragmented landscape, opportunities for dispersal to new sites and inter-population genetic exchange are minimal, which may limit its capacity to adapt to climate change. Given strong statewide and regional interest in developing conservation and monitoring programs for *C. candidum* (Anderson and Ruby, 2012; Minnesota Prairie Plan Working Group, 2011; MN DNR, 2014), and its likely sensitivity to localized climate change impacts, particularly as mediated through impacts on local groundwater (for which specific projects are rarely available), this orchid is a suitable model species for exploring the applications of linked habitat suitability and population models to site- and population-level adaptation planning.

2. Methods

2.1. Study site

We modeled *C. candidum* populations within Expandere Wildlife Management Area (WMA) in Cottonwood County, southern Minnesota

(Fig. 1). Managed by the Minnesota Department of Natural Resources, this 363-ha tallgrass prairie and wetland reserve is situated within a glaciated region of calcareous till that is currently intensively farmed (Appendix A.1). The reserve has an elevational range of 428 m to 442 m. A low-order stream bisects the property, and a ridge of sandy well-drained soils to the southwest appears to serve as a recharge area, providing moisture to a discharge area extending through the central portion of the site. Common soils include poorly to very poorly drained fine loam and clay loams over gravelly sand, frequently flooded in low areas. Well-drained to excessively drained sandy loam over gravelly sand occurs on scattered low rises. Projected regional climate change impacts expected to affect local plant communities include increased severe drought frequency, water table drawdowns and soil drying due to higher temperatures and increased evapotranspiration losses, and increased spread of invasive plant species (Galatowitsch et al., 2009).

C. candidum at Expandere WMA occurs in a relatively intact wet prairie within an apparent groundwater discharge area. Nearly 10,000 *C. candidum* plants were observed in a 2012 census, making the Expandere population potentially the largest in the state (Anderson and Ruby, 2012) and within its global range (MN DNR, 2014). Identified as an important indicator of high quality prairie and intact hydrology (Minnesota Prairie Plan Working Group, 2011), *C. candidum* is sensitive to drainage (Curtis and Greene, 1953) and shading by shrubs and invasive perennials (Curtis, 1946), both of which are expected to be exacerbated by regional climate change impacts (Galatowitsch et al., 2009). At Expandere WMA, the primary invasion threats to *C. candidum* include *Phalaris arundinacea* L. and expansion of shrubs. Other than fire and occasional haying, *P. arundinacea* at Expandere WMA is not specifically managed (R. Markl, pers. comm.). Because this population of *C. candidum* occurs at neither the southern nor northern edge of its range, climate change-driven increases in average and seasonal temperature are not likely to directly impact population persistence. Instead, changes in temperature and precipitation are expected to be mediated indirectly through their combined effects on groundwater availability and through changes in severe drought frequency.

2.2. Modeling approach

To investigate how interactions between regional climate change impacts, site features, and management might affect the viability of *C. candidum* at Expandere WMA, we created a linked population model and dynamic habitat suitability model using the metapopulation modeling software, RAMAS GIS (Akçakaya, 2005). The stage-structured population model allowed us to synthesize existing data and best estimates of *C. candidum* population dynamics (e.g. stage-specific survival, fecundity, and dispersal rates, and stochasticity in response to environmental fluctuations and extreme climatic events, specifically severe drought), and project meta-population trajectories and risks of decline. The habitat suitability model combined environmental spatial data with *C. candidum* occurrence data to identify patches of suitable habitat at Expandere WMA, which were linked via a dispersal matrix. The resulting metapopulation spatial structure was linked to the *C. candidum* population model, such that patch characteristics (e.g. carrying capacity) could influence population dynamics at a patch (i.e. subpopulation) scale. Finally, we modeled future climate change and management scenarios by creating time-series of habitat suitability maps that were linked to the population model via temporal trends in carrying capacity and vital rates.

2.3. Population model

We constructed a stochastic, spatially-explicit, stage-based population model for *C. candidum* in RAMAS GIS (Akçakaya, 2005), parameterized with demographic data estimated from literature review (Appendix, Table A1), expert knowledge, and field surveys (Anderson and Ruby, 2012). The model included 18 stages, including seed, protocorm (underground bulb), non-reproductive juveniles, reproductive adults, and dormant phases of juveniles and adults (Fig. 2). Protocorm, juvenile, and adult phases were subdivided into multiple stages to account for the slow rate of maturation, increasing rates of survival (S) and fecundity (F), and decreasing rates of dormancy as the plant matures (Appendix, Table A2). Density dependence in juvenile and adult stages was included as a ceiling model, such that abundances were reduced if they exceeded carrying capacity (K). We included demographic and environmental stochasticity in the model, and modeled seed dispersal from one population to another with a distance-dependent function (Appendix A.2).

The effects of severe drought were included in the model using RAMAS' "Catastrophe" function. For the baseline model (i.e. representing current conditions), we specified an annual probability of severe drought as 0.07 (approximately 1 in 14 years), reflecting historical frequencies for SW Minnesota (National Climatic Data Center, 2014). Probabilities were increased in the first and second years following a drought event (0.3 and 0.15, respectively) to simulate periodic multi-year drought events.

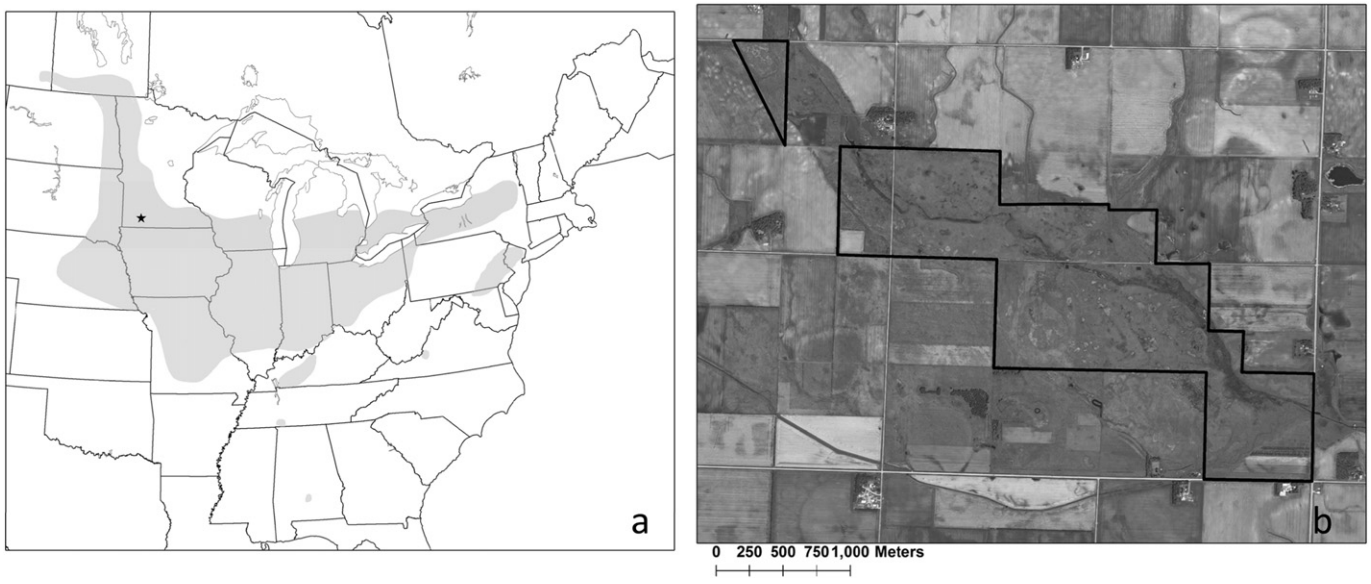

Fig. 1. Map of North America (a) showing *Cypripedium candidum* range in gray shading and location of model system study area, Expandere WMA, indicated with a star; and aerial view of Expandere WMA (b).
Range map is a composite modified from Romero-González et al. (2003), Smith (2012), and USDA NRCS (2014b).

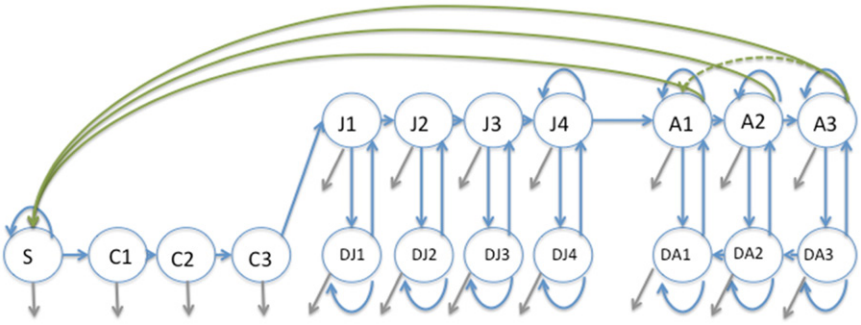

Fig. 2. *Cypripedium candidum* population model. Stages include seed (S); protocorm (underground bulb; C); non-reproductive juvenile (J); reproductive adult (A) and dormant phases of both juveniles and adults (DJ and DA, respectively). Green arrows represent fecundity (seed production); dashed arrows represent vegetative reproduction; blue arrows represent survival (transitions to the next stage or stay-in-stage transitions); and gray arrows represent mortality.

We estimated stage-specific impacts of drought, including decreasing fecundity, germination, and seedling survival by 80%; increasing dormancy rates by 80% and 90% of survival rates for juvenile and adult stages, respectively; slowing growth (increased stay-in-stage transitions relative to transitions to the next stage), and curtailing vegetative reproduction (Appendix, Table A3).

2.4. Habitat suitability model

We constructed a habitat suitability model in RAMAS GIS in order to identify present (and potential future) locations of suitable *C. candidum* habitat across the site. We compiled spatial data for *C. candidum* occurrence, elevation, soils (including depth to water table), hydrologic features, and invasive species cover at Expandere WMA in Arc GIS 10 (Appendix A.2). To calculate the probability of *C. candidum* occurrence in relation to influential spatial variables, we extracted spatial data and *C. candidum* presence/absence values for each cell in a 100 m-resolution grid overlaying the site and used stepwise logistic regression (SAS 9.3) to generate a habitat suitability function (Appendix A.2). Soil drainage class data were included as a class variable, while all other variables were continuous. Model selection was based on the Akaike information criterion (AIC).

In RAMAS GIS, we developed a map of suitable habitat at Expandere WMA that would serve as the metapopulation structure for the baseline *C. candidum* population model. We input the unstandardized habitat suitability function and relevant spatial layers (rasterized to a resolution of 0.03 km) to identify patches of suitable habitat and calculate average and total habitat suitability (ahs and ths, respectively) and carrying capacity (K) for each patch (Appendix A.2). When linked to the *C. candidum* population model, metapopulation structure (i.e. patch number and location) influenced dispersal outcomes, and patch characteristics (i.e. K) influenced density-dependent population growth.

2.5. Future scenarios

We designed future scenarios reflecting changes in drought frequency, increased depth to water table, and different configurations of increased invasive species cover (Table 1). Specific projections of how regional climate change will affect severe drought frequency and local groundwater availability are lacking, so we selected values that bracket a range of reasonable impacts under the A2 emissions scenario (Galatowitsch et al., 2009; IPCC, 2001). We combined future climate change and invasion effects in a factorial design ("primary scenarios"), and included "extreme" increase in drought frequency with only a subset of scenarios, resulting in a total of 54 scenarios including the baseline model. Drought frequencies were increased or decreased in decadal increments by adjusting annual probabilities and multi-year drought probabilities within the metapopulation model. We generated future scenarios for depth to water table and invasion by creating modified spatial layers for each decade in Arc GIS 10 and using the Habitat Dynamics Program in RAMAS GIS to calculate changes in habitat suitability (i.e. temporal trends in metapopulation structure and patch characteristics); effects on *C. candidum* survival and fecundity were modeled as functions of average habitat suitability (Appendix A.2). Due to the proprietary nature of rare species data included in the habitat suitability model, resulting maps illustrating current and potential future locations of *C. candidum* at Expandere WMA are not provided herein.

2.6. Simulations

We ran the baseline model (representing current conditions) and simulated future scenarios 1000 times, each for a duration of 100 years (i.e. 2012–2112). We chose a relatively long timeframe for the simulations to account for the long lifespan of *C. candidum* (Nicole et al., 2005). All simulation results were expressed in terms of juvenile and adult plants only (i.e. seed and protocorm stages were excluded), with an estimated initial abundance of 10,310 plants (Appendix A.2). We specified an extinction threshold of 50 individuals based on estimated minimum viable population size for similar species (e.g. Bowles, 1999) and evaluated population viability using mean final abundance, expected minimum abundance (EMA), and the probability that the population would decline by 50 or 90% from its original abundance at the end of the simulation. Mean abundance is the average population size at the end of a simulation, whereas EMA is the average minimum abundance throughout a simulation. EMA reflects how changes in a parameter move a population closer to (or further from) extinction and is particularly effective at summarizing risks of decline when the overall risk is low (McCarthy and Thompson, 2001). We conducted a sensitivity analysis of the baseline model to determine its sensitivity to stage matrix parameters, standard deviations, and drought probabilities and multipliers (Appendix A.3).

3. Results

To evaluate the impacts of multiple, interacting climate change and management effects on the *C. candidum* population at Expandere WMA, we first present results of the baseline model (representing current conditions). We then compare future scenario results to baseline model results, first examining the impacts of individual effects (e.g. increased drought frequency); second, impacts of two-way interactions between climate change and management effects (e.g. increased drought and depth to water table in combination); and finally, the impacts of three-way interactions between changes in drought frequency, increased depth to water table, and increased invasion cover.

Table 1
Climate change and management effects, levels, abbreviations, and descriptions. In future drought frequency scenarios, annual probability of severe drought is increased or decreased relative to the baseline model; *Cypripedium candidum* stage matrix parameters are multiplied by drought impact multipliers in severe drought years (see Tables A2 and A3). Increased depth to water table and invasion/management scenarios affect *C. candidum* fecundity and survival rates via changes in average habitat suitability relative to the baseline model. Effects were combined in a factorial design, with the exception of extreme increase in drought (included in only a subset of combinations), resulting in 54 total scenarios.

Effects & levels	Abbr.	Description
Drought frequency		
Baseline		Annual probability of severe drought: 0.07 (~1 in 14 years); probability in first and second years following drought: 0.30 and 0.15, respectively
Decreased frequency	Drt − 50	Baseline drought probabilities decreased by 0.1 per decade, from years 10 through 50. Final annual probability is 0.036 (~1 in 28 years)
Moderate increase	Drt + 50	Baseline drought probabilities increased by 50% in decadal increments (0.1 per decade, years 1–40), then held constant. Final annual probability is 0.105 (~1 in 9.5 years)
Large increase	Drt + 100	Baseline drought probabilities increased by 100% in decadal increments (0.2 per decade, years 1–40), then held constant. Final annual probability is 0.14 (~1 in 7 years)
Extreme increase	Drt + 200	Baseline drought probabilities increased by 200% in decadal increments (0.1 per decade, years 1–40), then held constant. Final annual probability is 0.21 (~1 in 4.8 years)
Depth to water table		
Baseline		Current depth to water table derived from soil data
Moderate increase	DW_15	Depth increased by 15 cm over 50 years, then held constant for 50 years
Large increase	DW_30	Depth increased by 30 cm over 50 years, then held constant for 50 years
Invasion/management		
Baseline		Current invasive species cover
Patch expansion	PE	Current invasion patches expand by 50% over 50 years (+10%/decade), then held constant for 50 years
Core invasion	CI	Invasion of core *C. candidum* population, equaling 50% increase in total invasion area over 50 years (+10%/decade); then held constant for 50 years
Reverse core invasion	Rev_CI	Invasion of core *C. candidum* population, equaling 30% increase in total invasion area over 30 years (10%/decade); decreased by 10%/decade for 30 years; then held constant at 0% invasion

3.1. Baseline model results

In the baseline model, mean abundance of *C. candidum* increased by 18% over 100 years and had an expected minimum abundance of 6874 (Fig. 3). The probability of declining by 50% was very low (3%). The baseline habitat suitability model identified 20 patches of suitable habitat; the current *C. candidum* population occupies the largest and highest quality of these patches (hereafter "core patch"; Table 2). Other identified patches were substantially smaller and of poorer quality; median habitat suitability for all patches was 0.07, whereas average habitat suitability for the core patch was 0.45. Due to low dispersal rates and low survival from seed stages, none of the other patches were substantially occupied by the end of the simulation (e.g. average final abundance of the nearest suitable patch was 1.38 individuals); thus reported metapopulation results represent the trajectory and risks of the core *C. candidum* patch almost entirely. According to the sensitivity analysis, baseline model outcomes are highly sensitive to changes in survival rates, particularly of the adult stage classes, and moderately sensitive to changes in drought probabilities and multipliers (Appendix A.3, Table A4).

3.2. Scenario results

None of the 54 scenarios combining climate change and invasion effects drove the population below the extinction threshold of 50 individuals, but scenarios did vary substantially in their impacts on habitat suitability, population trajectories, and estimated risks of decline. Among the primary set of scenarios (e.g. factorial combinations of effects), the three main effect levels with the greatest impact were core invasion, large increase in drought frequency (+100%), and large increase in depth to water table (+30 cm). Extreme increase in drought (+200%) had the most severe impacts across all measures.

Although expansion of invasive species patches had only a modest negative effect on habitat suitability and the *C. candidum* population, invasion of the core population resulted in a 49% decline in ths (Table 2), a 69% decline from the initial abundance of *C. candidum* and an EMA of 2779 (Fig. 3). When core invasion was reversed beginning in year 30, there was a 25-year lag in observable impacts on the population trajectory, and the population regained only about 1000 plants by the end of the simulation. However, reversing core invasion substantially reduced the probability of a 50% decline (18% vs. 96% for reverse core invasion and core invasion, respectively) and increased EMA to 4627.

Individually increasing depth to water table and increasing frequency of drought both had a negative impact on the *C. candidum* population (Fig. 3). Increases in depth to water table of 15 and 30 cm resulted in a 35% and 64% decline in core patch ths, respectively, and an even faster rate of decline (51% and 84%, respectively) in ths of the patch with the next highest suitability (e.g. the most likely on-site refuge) (Table 2), while as a regional "event", drought did not affect habitat suitability calculations. However, with the exception of extreme drought, these two types of effect – long-term, fine-resolution spatial changes vs. regional events – did not differ markedly in their impact on *C. candidum* trajectories. A 15-cm increase in depth to water table had very similar impacts as a 50% increase in drought frequency; in both cases, declines from the initial population were not apparent for 35–40 years, but the final mean abundance was approximately half that of the baseline model. Similarly, a 30-cm increase in depth to water table had comparable effects to a 100% increase in drought frequency. Population declines were apparent earlier (20–25 years) relative to the more modest depth and drought scenarios, and the final mean abundance was approximately 30% of that of the baseline model. Doubling the rate of increase in depth to water table (from 15 to 30 cm) or the frequency of drought (50% to 100%) resulted in greater than 30% reduction in EMA and approximately twice the probability of a 50% decline in abundance. Extreme drought (+200%) had a rapid and severe impact on the *C. candidum* population, resulting in an EMA of 991 individuals and a 62% probability of declining by 90% of the initial abundance (Appendix, Table A5).

On the other hand, a 50% decrease in drought frequency had a pronounced positive impact on the *C. candidum* population trajectory, the final mean abundance exceeding that of the baseline model by 30%. However, the relative benefits of a decreased drought frequency were smaller in magnitude than the negative impacts of increased drought frequency. For example: increasing drought frequency by 50% resulted

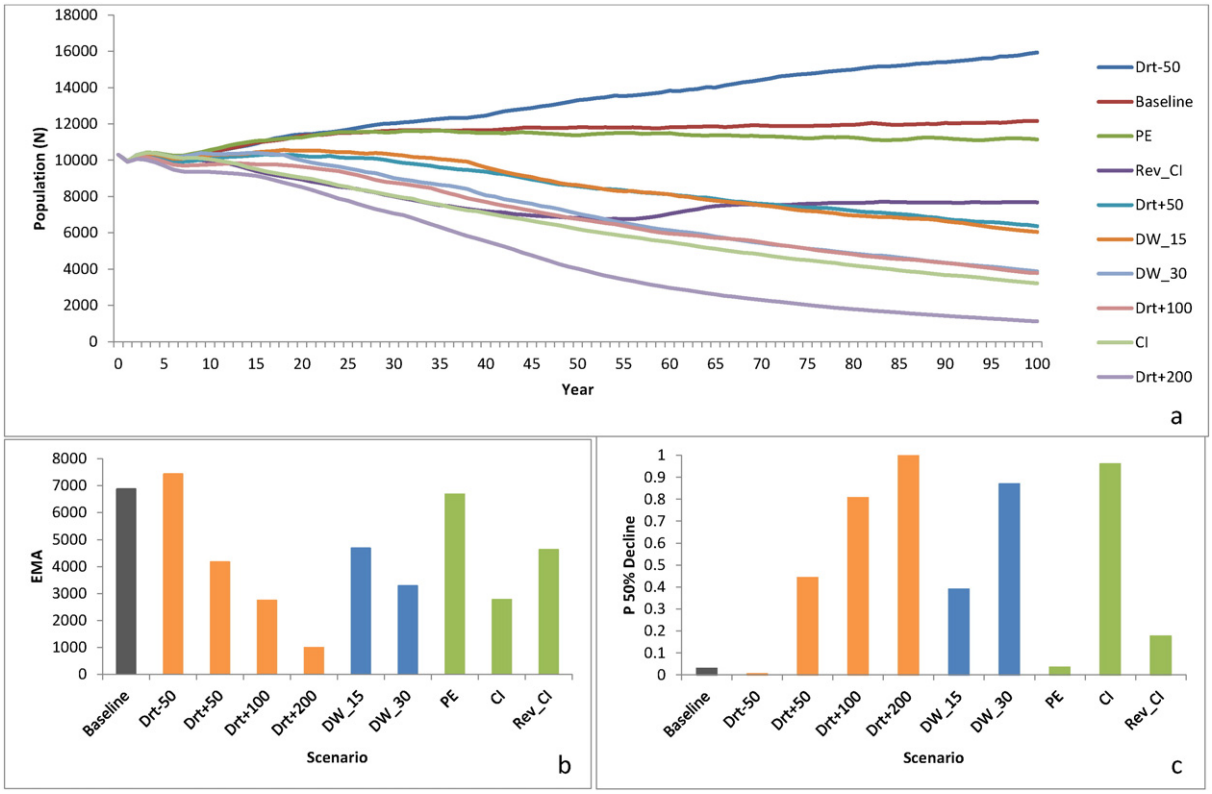

Fig. 3. *Cypripedium candidum* population responses to individual climate change effects (i.e. main effects), including changes in drought frequency (Drt), increasing depth to water table (DW), and different configurations of invasion and management (PE, CI, and Rev_CI). Results shown are: a) mean population trajectories; b) estimated minimum abundance (EMA); and c) probability of a 50% decline from initial abundance.

in an EMA 60% lower than the baseline model, but decreasing the drought frequency by 50% resulted in an EMA only 8% higher than the baseline model.

Scenarios that combined multiple climate change effects generally resulted in steeper declines in habitat suitability and *C. candidum* abundance and higher estimates of risk, and the mitigating effects of a decreased drought frequency were modest. Increasing drought frequency and depth to water table simultaneously resulted in greater than 80% probability of a 50% decline from the initial abundance (Fig. 4), while an increase in depth to water table combined with a decrease in drought frequency resulted in lower risks of decline. For example, there was an 87% probability of a 50% decline in abundance when a 30-cm increase in depth to water table occurred alone, while the probability of decline was only 61% when the same increase in depth to water table occurred with a 50% decrease in drought frequency. However, even with this mitigating impact of decreased drought, the final mean abundance in this combination scenario was only 40% that of the baseline model. In other words, decreasing drought frequency was not sufficient to prevent population decline in a future with increasing depth to water table.

Invasion of the core *C. candidum* population exacerbated impacts of both increased drought frequency and depth to water table, while patch expansion had minimal impact when combined with other climate change effects (Appendix, Table A5). Increased drought frequency not only exacerbated the negative effects of core invasion, but also suppressed the population's capacity for recovery when core invasion was reversed. When invasion reversal was combined with decreased

Table 2
Habitat suitability characteristics for *Cypripedium candidum* at Expandere WMA in response to modeled climate change scenarios, including number of suitable patches, total habitat suitability (ths), total patch area (ha), and median habitat suitability (mhs) for the site; ths, patch area, and average habitat suitability (ahs) for the core *C. candidum* population and the most suitable potential refuge; and the number of current *C. candidum* occurrence points located in unsuitable habitat (out of patch).

Scenario	Site (metapopulation)				Core *C. candidum* population				Potential refuge		
	# patches	ths	Total patch area (ha)	mhs	ths	Patch area (ha)	ahs	# out of patch	ths	Patch area (ha)	ahs
Baseline	20	457	157	0.07	355	71	0.45	2	55	25	0.20
PE	22	428	152	0.06	345	72	0.43	2	50	24	0.19
CI	20	281	154	0.06	180	68	0.24	2	55	25	0.20
Rev core (Y30)	20	300	154	0.07	197	68	0.26	2	55	25	0.20
DW_15	21	269	116	0.03	230	63	0.33	4	27	20	0.12
DW_30	12	137	59	0.04	127	46	0.25	14	9	10	0.08
DW_15 * PE	16	252	106	0.03	219	63	0.31	5	24	19	0.11
DW_30 * PE	13	128	58	0.03	117	45	0.23	14	8	10	0.07
DW_15 * CI	22	116	113	0.03	77	60	0.12	4	27	20	0.12
North unit					57	30	0.17				
South unit					19	31	0.06				
DW_30 * CI	19	33	39	0.05	18	21	0.09	94	9	10	0.08
North unit					18	20	0.08				
South unit					0.4	0.36	0.10				

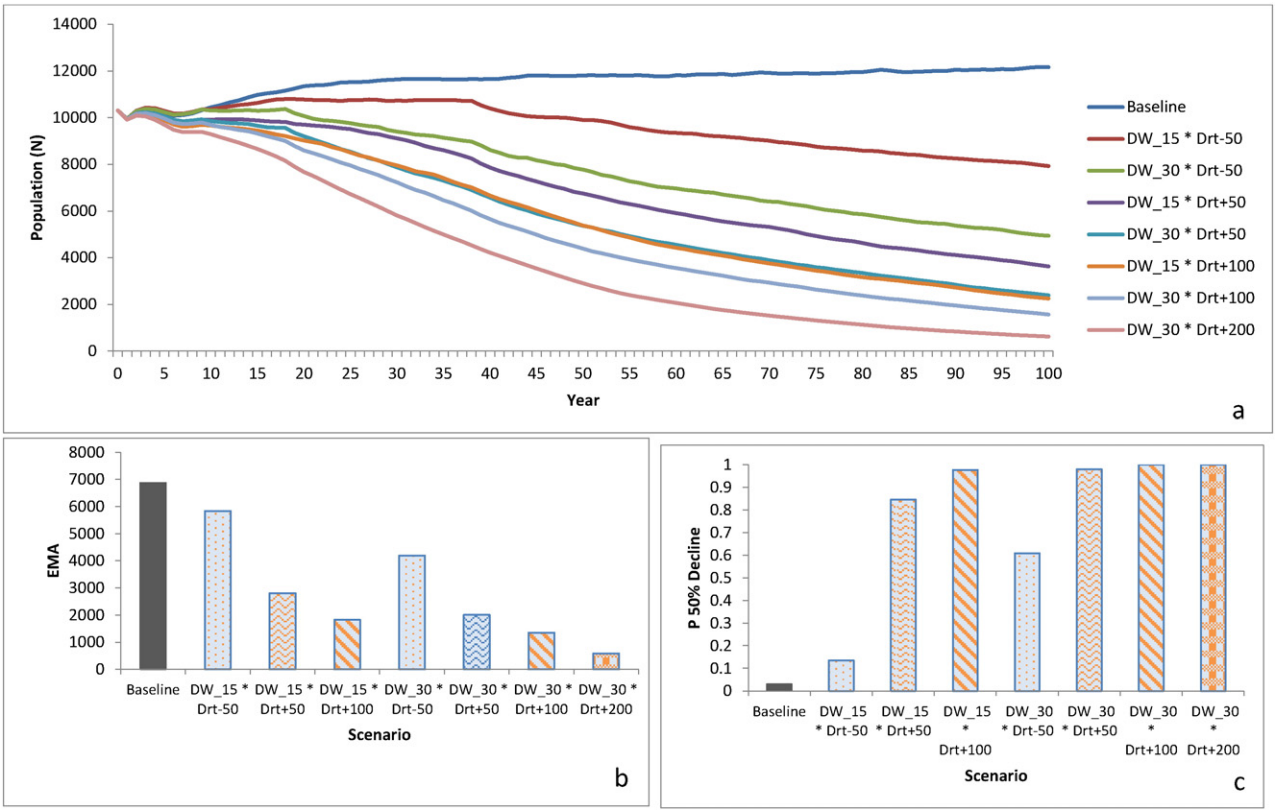

Fig. 4. *Cypripedium candidum* population responses to interactions between increased depth to water table (DW) and changes in drought frequency (Drt). Results shown are: a) mean population trajectories; b) estimated minimum abundance (EMA); and c) probability of a 50% decline from initial abundance.

drought frequency, the population nearly recovered to its original abundance, although mean final abundance remained lower – and risks of decline, higher – than those of the baseline model (Fig. 5). However, when combined with increasing drought frequency, the recovery phase following invasion reversal was short-lived, and the population continued to decline, resulting in a final mean abundance 57% lower than the initial abundance. When combined with the most extreme drought effect, reversing invasion had very little impact on population growth and risk of decline; the probability of a 50% decline was 100% regardless of whether invasion was reversed, and the risks of a 90% decline in abundance were 97% and 81% for core invasion and reverse core invasion, respectively.

In a similar manner, mean final abundance was lower and risks of decline were higher when core invasion was combined with increasing depth to water table, and the capacity for recovery following invasion reversal was substantially suppressed (Fig. 6). When core invasion occurred with a 15-cm increase in depth to water table, results were similar to combining core invasion with a 100% increase in drought frequency; likewise, combining core invasion with a 30-cm increase in depth to water table produced results approximately midway between the 100% and 200% increase in drought frequency. Even though, as main effects, moderate increases in drought frequency (+50%) and depth to water table (+15 cm) were comparable, and larger increases in drought frequency (+100%) and depth to water table (+30 cm) were comparable, when combined with core invasion, increasing depth to water table appeared to exacerbate impacts of invasion more than the comparable drought effect (Appendix, Table A5). Furthermore, when core invasion occurred in conjunction with decreases in depth to water table, the core population of *C. candidum* splits into two separate subpopulations, with the more densely populated southern unit experiencing steeper declines in habitat suitability (Table 2). With a 30-cm drop in water table, the southern unit nearly disappears, leaving 94 current *C. candidum* occurrence points (representing clusters of plants) in unsuitable habitat.

When all three climate change and management effects were combined (drought, depth to water table, and invasion), risks of population decline increased dramatically. Sixteen of the 20 scenarios with three-way interactions had greater than 98% probability of a 50% decline from the initial abundance (Appendix, Table A5). The majority of scenarios involving core invasion had a high probability of a 90% decline, the exceptions being those mitigated by a decreased drought frequency (−50%) and a more modest increase in depth to water table (15 cm) combined with invasion reversal (Fig. 7). Under the most favorable scenario (i.e. 15-cm increase in depth to water table, and decreased drought frequency), reversing core invasion allowed a recovery to 4662 individuals, nearly half the initial abundance. However, increasing either depth to water table or drought frequency further limited recovery. Under the most extreme scenario – core invasion, 30-cm increase in depth to water table, and a 200% increase in drought frequency – EMA and mean final abundance were both just over 200 individuals, and the probability of a 90% decline in abundance was 100%. Adding invasion reversal to those extreme conditions resulted in nearly double the mean abundance and EMA (418 and 397, respectively), but the probability of a 90% decline was still 99%.

4. Discussion

Developing and applying dynamic, linked, habitat suitability and population models allow us to prioritize management and monitoring approaches for our model system in light of multiple potential climate change impacts. We can evaluate the relative and cumulative influence of plant invasions, increasing depth to water table, and changes in severe drought frequencies on a globally important population of *C. candidum*, and use the model results to propose site-specific adaptation

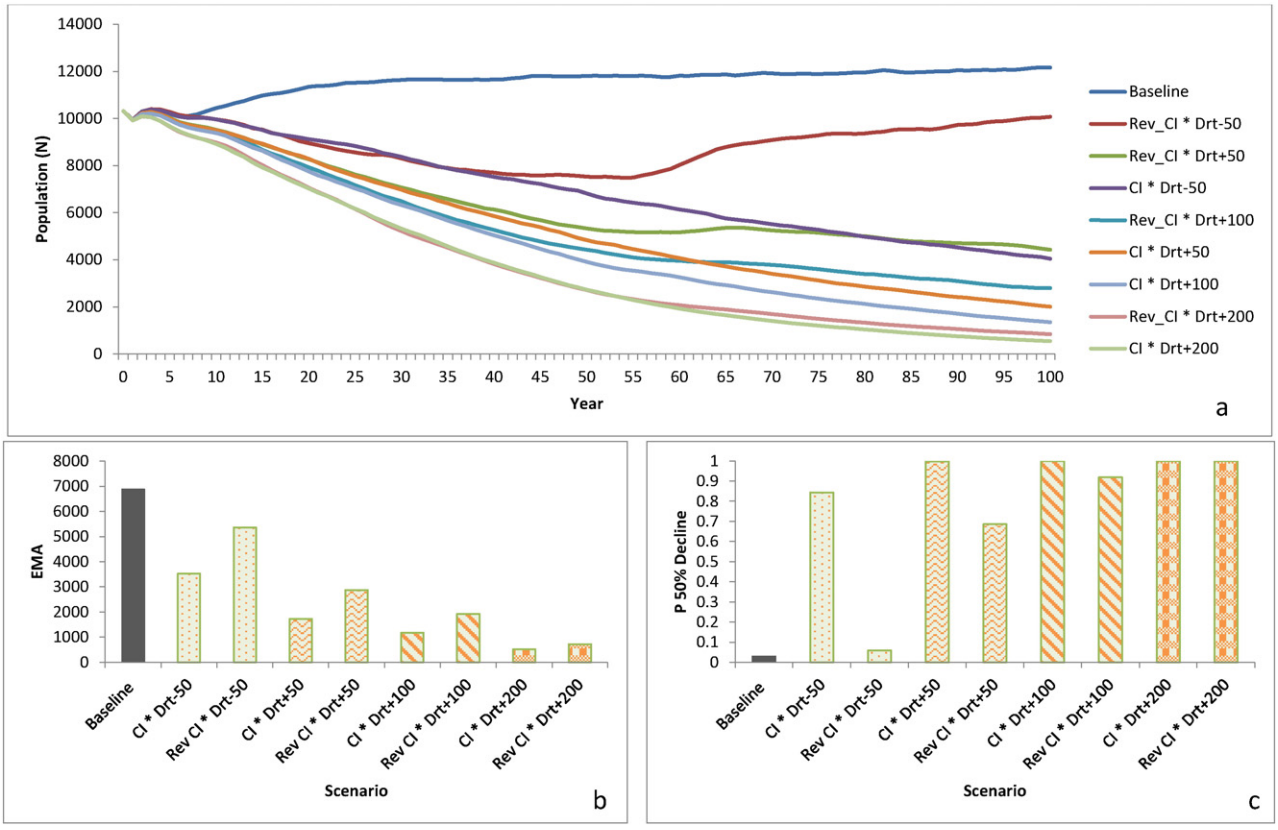

Fig. 5. *Cypripedium candidum* population responses to interactions between invasion/management effects (CI and Rev_CI) and changes in drought frequency (Drt). "Patch expansion" invasion scenarios are excluded. Results shown are: a) mean population trajectories; b) estimated minimum abundance (EMA); and c) probability of a 50% decline from initial abundance.

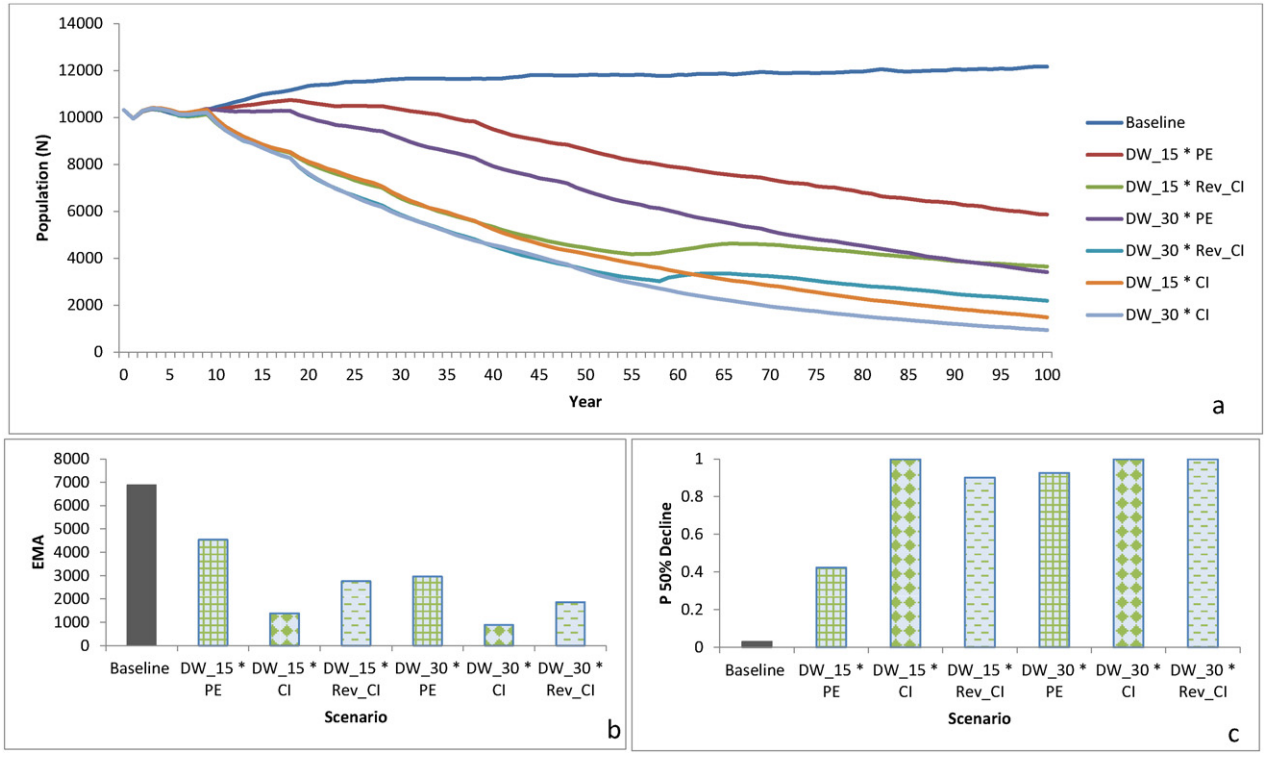

Fig. 6. *Cypripedium candidum* population responses to interactions between increases in depth to water table (DW) and invasion/management effects (PE, CI, and Rev_CI). Results shown are: a) mean population trajectories; b) estimated minimum abundance (EMA); and c) probability of a 50% decline from initial abundance.

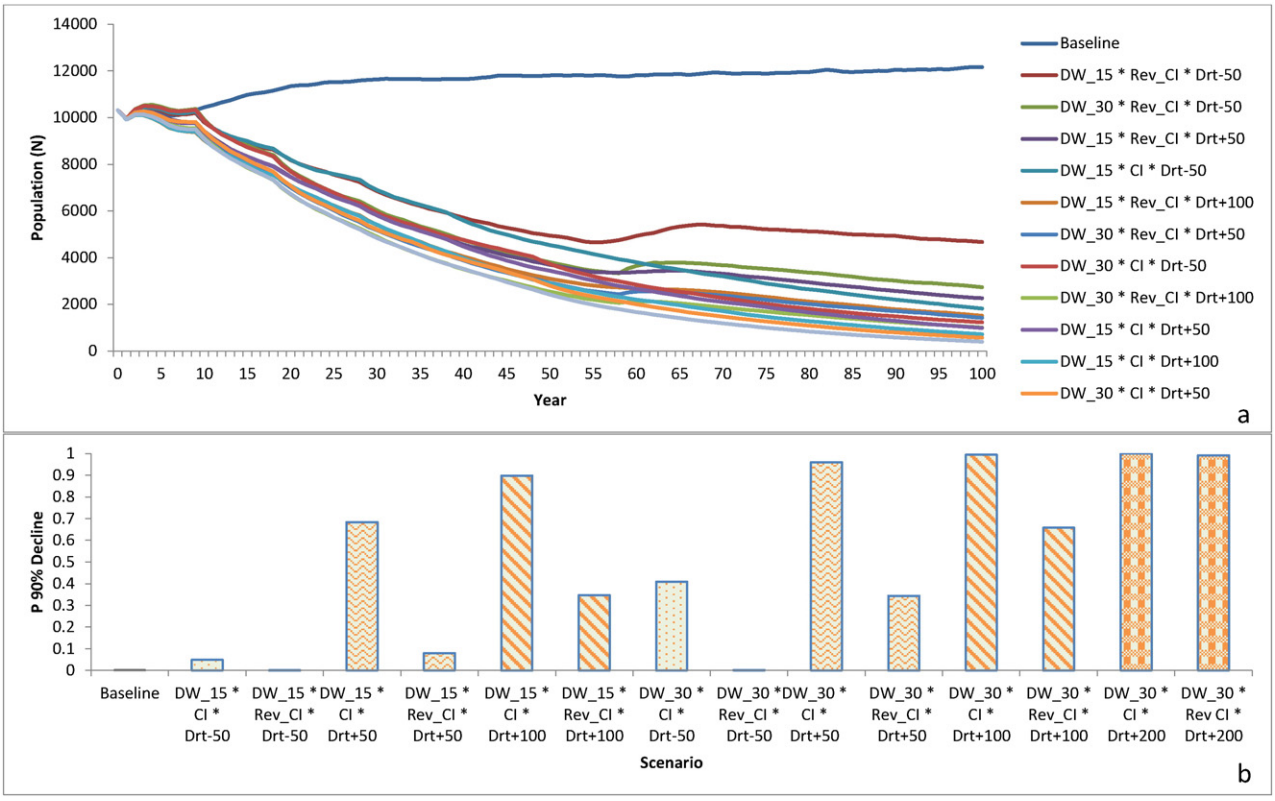

Fig. 7. *Cypripedium candidum* population responses to interactions between increases in depth to water table (DW), invasion/management effects (CI and Rev_CI) and changes in drought frequency (Drt). "Patch expansion" invasion scenarios are excluded. Results shown are: a) mean population trajectories; and b) probability of a 90% decline from initial abundance.

strategies and monitoring guidelines. The potential to inform decisions about adopting low-risk versus high-risk adaptation strategies is particularly valuable, given that conservation decision-makers are often hesitant to shift to high-risk strategies in the face of uncertainty (Lawler et al., 2010). For this reason, we find the modeling approach to be particularly effective for developing conservation strategies for rare and vulnerable species, for which the need to minimize risk is particularly critical.

This modeling approach effectively informs conservation decision-making by providing the capacity to assess multiple interacting stressors at the local scale, identify the most important stressors, and evaluate the efficacy of management strategies in light of their cumulative impacts. Applying this process to prioritize adaptation strategies is critical, because while conservation actions are often directed at individual stressors, interactions between climate change, land-use, invasive species, and other stressors can exacerbate threats to conservation targets (Lawrence et al., 2014) and render individual conservation strategies ineffective (Bonebrake et al., 2014). In our model system, although no single type of stressor emerged as having the greatest influence on *C. candidum*, combining multiple stressors provides more nuanced insights. For example, increasing the frequency of regional drought events and gradually increasing depth to water table at a finer spatial scale have remarkably similar effects on the *C. candidum* population trajectory and risk estimates (Fig. 3). However, the cumulative impacts of increased drought and depth on *C. candidum* are 30–50% greater than individual effects (Figs. 3 and 4), and when combined with other stressors (e.g. core invasion), increasing depth to water table appears to exacerbate impacts on *C. candidum* more strongly than drought (Figs. 5 and 6). This suggests that while both types of climate change effects are important, prioritizing strategies that minimize water table drawdowns over drought resistance strategies may be critical, particularly given that water table drawdowns could further increase invasibility of *C. candidum* habitat.

By exploring population responses to a broad range of future climate and management scenarios, we can more effectively prioritize site-specific management strategies. Relatively "low-risk" resilience strategies, such as invasion prevention and management, are important initial actions for reducing the impacts of climate change on vulnerable populations (Galatowitsch et al., 2009), as evidenced by our model system. Preventing invasion of the core *C. candidum* population is clearly an essential resilience strategy, as the core invasion scenario has a greater negative impact on *C. candidum* population growth and risks of decline than all scenarios other than the extreme drought scenario. The negative effects of invasion persist, even after core invasion is reduced to current levels, and the capacity for population recovery is even further limited when invasion is combined with other climate change stressors, suggesting that prevention, early detection, and rapid response to invasion of core *C. candidum* habitat are paramount. Invasion management is a palatable adaptation strategy for many managers, because it is already a familiar tool in the conservation toolbox, and it is relatively robust to the uncertainties of climate change (Lawler et al., 2010). However, it is important to recognize that adopting a familiar, low-risk, resilience strategy is not equivalent to simply maintaining a management status quo; as climate change may accelerate invasions in plant communities, even low-risk resilience strategies may need to be revised and intensified to keep pace with climate change and its indirect biotic effects. At Expandere WMA, for example, increased flooding and storm events (not included in our model) may increase the spread of *P. arundinacea* – a primary invasion threat in *C. candidum* habitat – and fluctuating water tables are likely to favor its establishment. Therefore, preventing invasion of the core *C. candidum* population will likely require increasingly intensive invasion management and monitoring.

Furthermore, as we found in our model system, low-risk resilience strategies such as invasion management are unlikely to be sufficient for preventing population decline under climate change; "high-risk" strategies must be given serious consideration as well. Preventing core

invasion alone, for example, does not prevent substantial declines in *C. candidum* abundance in the face of increased drought frequency or depth to water table. In order to sustain current levels of *C. candidum*, state decision-makers and site managers may need to adopt strategies that address these direct impacts of climate change, such as enacting and enforcing sustainable water use policies (van der Knaap et al., 2014), protecting critical recharge zones, or even irrigating *C. candidum* populations to resist drought impacts. One of the valuable outcomes of building the habitat suitability model for *C. candidum* is the identification of important recharge areas in unprotected land adjacent to the WMA. Protecting these key recharge areas, through land acquisition or via cooperative agreements with local landowners, could slow the rate of water table drop and maintain habitat suitability in the discharge areas occupied by *C. candidum*. Land acquisition and protection strategies are typically costly and politically challenging, but models can guide the allocation of limited resources so that investments made have the greatest likelihood of achieving conservation aims (Conlisk et al., 2014; Miller et al., 2009; Wintle et al., 2011).

Facilitation strategies, such as transplanting individuals into future climate refuges, are also perceived as high-risk, because their outcome depends on the precise nature and magnitude of climate change impacts (Lawler et al., 2010), but linking dynamic spatial data to population models can reduce risks both by projecting timelines for population responses to climate change and management, and by identifying potential refuges. While most analyses of "assisted colonization" evaluate translocations to future off-site refuges (Regan et al., 2012), modeling at finer spatial resolutions allows for identification of potential on-site refuges, thereby enabling lower-risk, short-distance translocations within a protected site. Unfortunately, although our model identified 19 additional patches of suitable *C. candidum* habitat at Exapandere WMA, these patches were even more vulnerable to climate change than the original population (Table 2), suggesting that they were unlikely to be sustainable refuges. Closer examination of habitat suitability maps, however, suggests that some on-site translocations might be worth considering. Specifically, the northern portion of the *C. candidum* patch appears to maintain higher average habitat suitability than the southern unit, which currently supports the highest density of *C. candidum* at Expandere WMA. In fact, some climate change scenarios resulted in substantial patch contraction along the southern edge, leaving numerous orchid plants "stranded" in unsuitable habitat (Table 2). A relatively low-risk facilitation strategy for *C. candidum* at this site would therefore be to translocate individuals from the southern edges of the patch to the northern unit, if the projected declines are observed.

In addition to informing management decisions, linked habitat suitability and population models provide crucial insights that inform development of strategic and efficient monitoring programs. Population monitoring can generate much-needed biological data at resolutions and time-scales appropriate for predicting species' vulnerability to climate change (Staudinger et al., 2013), however, such monitoring is often time-intensive and is seldom adequately funded. Models can increase the applicability and cost-effectiveness of monitoring by identifying key parameters and anticipated timelines for population responses. For example, we used sensitivity analyses to identify *C. candidum* life stages and transition rates to which model outcomes are most sensitive (e.g. juvenile and adult survival), and recommend a monitoring focus on these parameters. Monitoring belowground life stages is particularly challenging, but model results are relatively insensitive to seed and protocorm survival. The model is, however, sensitive to larger increases in dormancy rates, suggesting that annual census and targeted "mark-recapture" analyses to track individuals moving in and out of dormancy (Shefferson, 2006) may be a worthwhile investment. Long-term, relatively high-resolution monitoring will be required to detect *C. candidum* responses to climate change and management through the "noise" of dormancy and across lags in population responses observed in our model results. Such intensive monitoring is not feasible for all *C. candidum* populations, but intensively monitoring a few key populations will likely yield more useful information than superficially monitoring many populations.

Monitoring results, including field observations of climate change impacts and population responses, are not only useful for validating and improving models, but are also an essential component of effective adaptive management, which allows for informed, strategic, and flexible decision-making under uncertainty (Lawler et al., 2010). Monitoring and evaluation provide the feedback loop by which management can be revised in response to observed climate change impacts and population responses. Linked spatial and population models can therefore play an important role in adaptive management by informing selection of adaptation strategies as well as monitoring protocols for effective evaluation. For example, based on scenario results, we have developed specific adaptation strategies and monitoring recommendations for *C. candidum* at Expandere WMA (Table 3). The specificity of recommendations that emerge from this modeling approach makes them directly applicable to conservation decision-making at the site scale. Although, to some extent, these recommendations can be applied to other *C. candidum* populations, and – even more generally – to conservation of wet prairie habitat and associated species, constructing site-specific spatial models is necessary to assess changes in habitat suitability and identify potential on-site refuges and key landscape features (e.g. recharge areas), and caution should be used when applying model results to other species, particularly those with very different life histories.

Although some barriers and information gaps present challenges to implementing this modeling approach, creative solutions can be applied to incorporate best available information into an effective decision-making tool. The unavailability of relevant species' biological data poses one of the greatest challenges to modeling impacts of climate change on specific species (Staudinger et al., 2013), particularly rare and vulnerable species. However, this lack of information need not preclude building a useful model. Although parameterizing models with detailed time-series of biological data collected via field studies and monitoring is certainly ideal, it is often unfeasible due to financial and logistical constraints, and delaying decision-making until such studies have been conducted may be even riskier than acting with incomplete information. As we have demonstrated, a useful model can be developed with data extracted from literature, expert knowledge, short-term field observations, and cautious extrapolations from data on comparable species. Sensitivity analyses can then be used to identify where uncertainty matters most, thus focusing future research efforts. Another

Table 3
Management and monitoring recommendations for *Cypripedium candidum* population at Expandere WMA based on linked habitat suitability and population models simulating climate change and management scenarios.

	Management & monitoring recommendations
1	Increase management intensity of existing *Phalaris arundinacea* on site; scout annually for invasion in core *C. candidum* population; implement *immediate* response if core invasion is detected.
2	Monitor changes in woody species cover in core area; establish cover threshold beyond which management intensity should be increased (e.g. increase burn frequencies and/or manually remove woody species).
3	Install groundwater observation wells to monitor changes in depth to water table across *C. candidum* habitat; evaluate rates of change to determine the model scenario to which observations are most closely aligned.
4	Begin planning for protection of key recharge areas, as identified by the spatial model.
5	Identify local water- and land-use policies and regulations that require revision and/or increased enforcement in order to mitigate declines in water table depth.
6	Monitor frequency of regional severe drought events and *C. candidum* responses to drought; consider developing pilot irrigation study to determine effectiveness of irrigating in drought years.
7	Monitor *C. candidum* population using protocol that allows detection of trends through variability (e.g. dormancy) and captures spatial distribution, with a particular focus on the potentially vulnerable southern edge; establish minimum population thresholds beyond which "high-risk" facilitation and resistance strategies (e.g. translocations; irrigation) should be implemented.

important barrier to developing site-scale habitat suitability models is the need for fine-resolution spatial data that can be linked to climate change projections. We found this to be an even greater challenge than the lack of detailed *C. candidum* data, but ultimately we developed a creative solution that merged published soils and elevation data to generate a fine-scale depth to water table layer. The use of scenarios to bracket potential climate change impacts was also an effective method for incorporating climate change uncertainty. Thus, despite these challenges, we were able to use our model to propose site-specific management and monitoring approaches for an important population of *C. candidum*, while also providing insights for assessing climate change adaptation in vulnerable wet prairie and meadow ecosystems. Certainly, developing such models requires time, data, and expertise that lie beyond the scope of many land managers; partnerships between management agencies and research organizations will therefore be an important component to using modeling more broadly to inform management. Although it is not feasible to develop linked habitat suitability and population models for an entire flora, applying this approach to high-priority populations and key species of interest will allow conservation planners and practitioners to move forward in making sound, on-the-ground management decisions in the face of climate change.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.10.010.

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