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Effects of climate change and anthropogenic modification on a disturbance-dependent species in a large riverine system

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Abstract. Humans have altered nearly every natural disturbance regime on the planet through climate and land-use change, and in many instances, these processes may have interacting effects. For example, projected shifts in temperature and precipitation will likely influence disturbance regimes already affected by anthropogenic fire suppression or river impoundments. Understanding how disturbance-dependent species respond to complex and interacting environmental changes is important for conservation efforts. Using field-based demographic and movement rates, we conducted a metapopulation viability analysis for piping plovers (*Charadrius melodus*), a threatened disturbance-dependent species, along the Missouri and Platte rivers in the Great Plains of North America. Our aim was to better understand current and projected future metapopulation dynamics given that natural disturbances (flooding or high-flow events) have been greatly reduced by river impoundments and that climate change could further alter the disturbance regime. Although metapopulation abundance has been substantially reduced under the current suppressed disturbance regime (high-flow return interval ~ 20 yr), it could grow if the frequency of high-flow events increases as predicted under likely climate change scenarios. We found that a four-year return interval would maximize metapopulation abundance, and all subpopulations in the metapopulation would act as sources at a return interval of 15 yr or less. Regardless of disturbance frequency, the presence of even a small, stable source subpopulation buffered the metapopulation and sustained a low metapopulation extinction risk. Therefore, climate change could have positive effects in ecosystems where disturbances have been anthropogenically suppressed when climatic shifts move disturbance regimes toward more historical patterns. Furthermore, stable source populations, even if unintentionally maintained through anthropogenic activities, may be critical for the persistence of metapopulations of early-successional species under both suppressed disturbance regimes and disturbance regimes where climate change has further altered disturbance frequency or scope.

Key words: *Charadrius melodus*; early-successional; endangered species conservation; floods; global change; land-use change; piping plovers; population viability analysis; succession; Vortex.

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INTRODUCTION

Resource management has historically followed a command and control approach in an effort to optimize economic gains and minimize unpredictable outcomes or events, such as insect outbreaks, fires, and floods (Holling and Meffe 1996). The result is most often “the pathology of natural resource management” where natural disturbances are suppressed, natural variation is reduced, and ecosystems become vulnerable to undesirable change (Holling and Meffe 1996, Seidl et al. 2016).

These types of ecosystem modifications have made disturbance-dependent organisms especially vulnerable to extinction (e.g., Brawn et al. 2001, Lawler et al. 2002), particularly species that evolved in landscapes with historically frequent disturbances (Martin and Fahrig 2016). Species in naturally disturbed ecosystems are adapted to a specific disturbance regime, which encompasses the frequency, timing, duration, and intensity of disturbances (Lytle and Poff 2004, Keely et al. 2011). Species adapted to historical disturbance regimes, whether related to fire, flooding, storms, or other natural disturbances, are often negatively affected by alterations to those regimes (Kelly et al. 2014, Ranius et al. 2014, McElderry et al. 2015, Paniw et al. 2015). Regime changes can accelerate shifts in species composition, alter biome boundaries, and lead to state changes and “no analogue” communities (Turner 2010).

In addition, interactions among multiple drivers are particularly common in disturbance-dependent ecosystems, where climate change-related shifts in precipitation and temperature are expected to affect extreme disturbance events (Intergovernmental Panel on Climate Change (IPCC) 2013) in ecosystems where natural disturbance regimes have already been suppressed. For instance, climatic shifts have resulted in higher wildfire frequencies, durations, and seasons in the western United States, where managed fire suppression has been the trend for decades (Westerling et al. 2006). Similarly, increased drought frequencies are expected to further stress ecosystems in impounded rivers worldwide (Palmer et al. 2008). Such interactions between land-use and a changing climate can cause major alterations to landscapes and the biological communities they support (Paine et al. 1998, Cochrane and Laurance 2008, Regos et al.

2015). Furthermore, stressed ecosystems are often less resilient to climate change impacts (Staudt et al. 2013). Therefore, understanding the complex interactions among climate, disturbance regime, habitat change, and associated biological assemblages will be critical for formulating effective climate change adaptation and restoration strategies.

We explored how a changing disturbance regime, related to both land-use management and climate change, could affect the extinction risk of a disturbance-dependent species on impounded, large floodplain rivers. Large floodplain rivers are among the most endangered ecosystems in the world, largely due to a loss of natural flow regimes and disturbances (Poff et al. 1997, Tockner and Stanford 2002, Peipoch et al. 2015). Flood pulses once universal in these ecosystems promoted the movement of organisms, nutrients, and soils while creating nutrient-rich mosaics of different successional habitats that supported diverse plant and animal assemblages (Junk et al. 1989, Poff et al. 1997, Amoros and Bornette 2002). Today, the majority of large floodplain rivers worldwide have been dammed, diverted, channelized, and/or pumped, which has dramatically altered flooding regimes, promoted terrestrialization, and reduced species richness throughout the ecosystem (Poff et al. 1997, Peipoch et al. 2015). Rivers and their ecosystems will likely be disproportionately affected by climate change; anthropogenic modifications have reduced their natural abilities to adjust to and absorb extended droughts or extreme precipitation events (Palmer et al. 2008).

We used 6 yr of observations of three piping plover (*Charadrius melodus*) populations on the Missouri and Platte rivers in the central United States (Fig. 1) to conduct a metapopulation viability analysis (PVA). During the study period, a large regional flood occurred for the first time in 13 yr and influenced movement, reproduction, and survival rates of the target species in one subpopulation (Catlin et al. 2015). This allowed us to measure vital rates as a function of time-since-disturbance and to model scenarios that assumed hypothetical changes (i.e., due to climate change) to the current, suppressed disturbance regime. These scenarios offer a “broad exploration of novel futures” (Seidl et al. 2016), and results have important implications for understanding population and metapopulation trends in dynamic

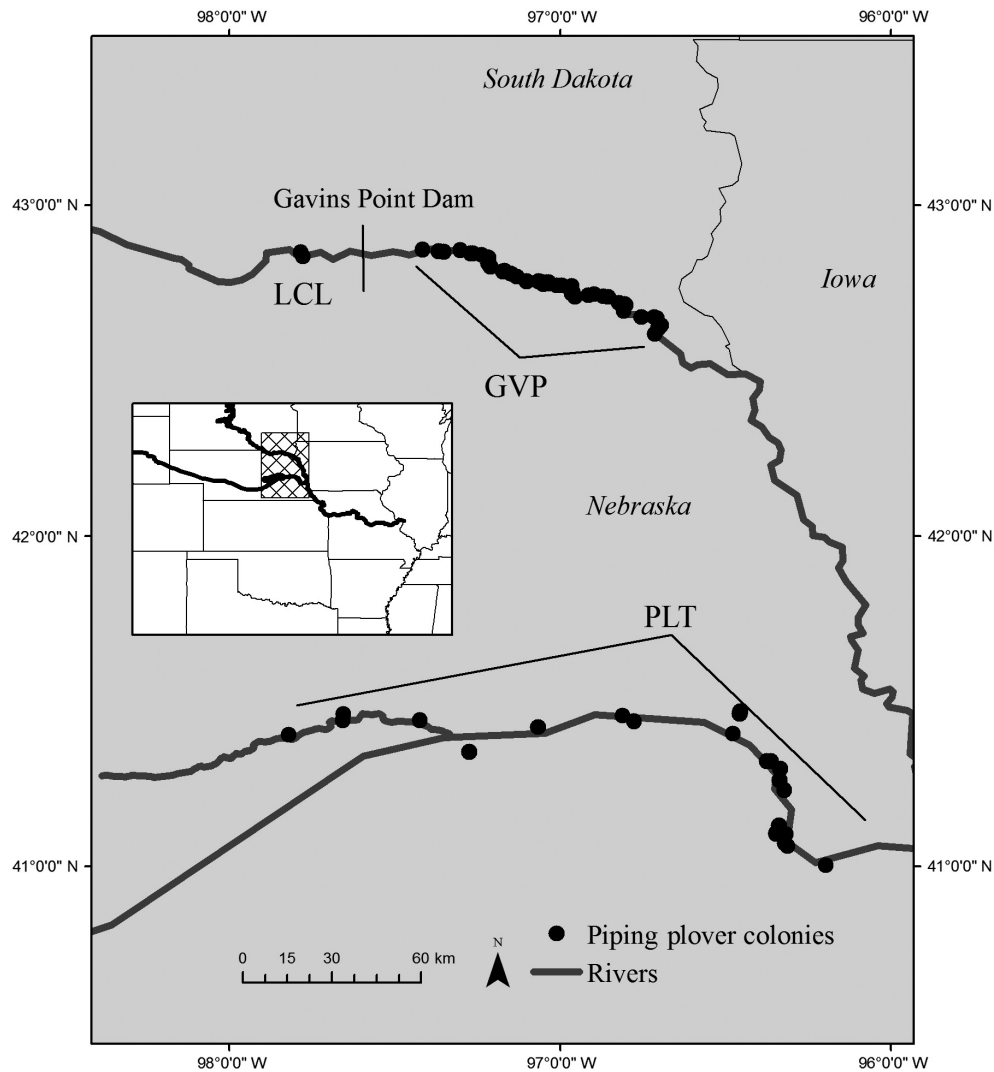


Fig. 1. The Missouri–Platte River piping plover (*Charadrius melodus*) metapopulation. The Lewis and Clark Lake (LCL) and Gavins Point Reach (GVP) subpopulations, separated by the Gavins Point Dam, are located on the Missouri River, while the Platte River subpopulation (PLT) is located on the Platte River.

systems where historical drivers of landscape change have been altered.

MATERIALS AND METHODS

Study system

Piping plovers are imperiled, migratory shorebirds with discrete breeding populations on the Atlantic Coast, the Great Lakes, and the Northern Great Plains of Canada and the United States. The metapopulation considered in this study, which supports approximately 14% of the

Northern Great Plains piping plover population (Elliot-Smith et al. 2009), was composed of three subpopulations on the lower Platte River (PLT) and the Missouri River at Lewis and Clark Lake (LCL) and Gavins Point Reach (GVP; Fig. 1).

Preferred nesting habitat for the species is open or sparsely vegetated expanses of flat, dry portions of sandbars and beaches in areas adjacent to water (Elliot-Smith and Haig 2004). Annual spring bankfull flows and higher-magnitude floods (hereafter, collectively referred to as “high flows” or “high-flow events”) historically created or

maintained open, early-successional habitat used by this and other species (Hesse and Mestle 1993, U.S. Fish and Wildlife Service 2009). Prior to 1952, when control of the Missouri River began with the construction of three main-stem dams, high-flow events with peak releases over 110,000 ft³/s and 160,000 ft³/s occurred in 15 and 4, respectively, of the 24 yr on record at the Omaha, Nebraska River gage (Hesse and Mestle 1993). However, the frequency of these processes was reduced as the Missouri and Platte rivers and their tributaries were channelized, dammed, and diverted (Lautrup and LeValley 1998, National Research Council 2005). For example, no peak releases over 160,000 ft³/s and only two events over 110,000 ft³/s were recorded at the Omaha gage in the 33 yr following main-stem dam closures in 1954 (Hesse and Mestle 1993). Today, high-flow events (e.g., peak discharge rates $\geq 100,000$ ft³/s; monthly outflows > 3 million acre-feet) occur approximately once every 20 years in the Missouri River portion of our study area (discharge rates from Gavins Point Dam available at <http://www.nwd-mr.usace.army.mil/rcc/projdata/gapt.pdf>). This reduction in high flows, and the habitat created by these events, has led to substantial declines in populations of piping plovers and over 80 additional species from a variety of taxa (National Research Council 2002, U.S. Fish and Wildlife Service 2009).

Under the current disturbance regime, open natural sandbars rarely occur upstream of the Loup River confluence in the Platte River (Elliot-Smith et al. 2009, Bomberger Brown et al. 2010), and most piping plovers in the PLT subpopulation now nest off-river on sites that include sand and gravel mines and lakeshore housing developments located on the river's floodplain (Bomberger Brown et al. 2010; Fig. 1). The GVP subpopulation lies within one of the last free-flowing portions of the Missouri River, and piping plovers within this subpopulation use both natural and engineered (i.e., mechanically maintained by the U.S. Army Corps of Engineers through dredging and vegetation management; Catlin et al. 2011) sand and gravel bars (Fig. 1). The LCL subpopulation is located in the reservoir impounded by the Gavins Point Dam on the Missouri River, and birds within this subpopulation primarily used engineered sandbars during our study (Catlin et al. 2016).

In June 2010 through 2011, historically high water releases from the Gavins Point Dam (peak

releases > 160,000 ft³/s; U.S. Army Corps of Engineers 2012) occurred following high levels of winter snow and spring rain. This flood submerged all active nests and chicks within GVP, eliminating reproductive output for this population in both years. The two high-flow years created an abundance of nesting habitat downstream from the dam for the 2012 and 2013 breeding seasons. LCL and PLT were largely unaffected by water fluctuations in 2010 and 2011, and birds within these subpopulations continued to rely on human-maintained habitats for nesting during our study period (Catlin et al. 2016). As a result of periodic high-flow events and successional processes, the carrying capacity of habitat used by GVP birds fluctuated widely during the study period on which our demographic model was based. In contrast and for reference, the amount of habitat available for individuals in LCL and PLT remained relatively constant during our study period, and these subpopulations were generally at or near carrying capacity (Catlin et al. 2015; D. H. Catlin, *unpublished data*, M. Bomberger Brown, *unpublished data*).

Disturbance regimes in the watershed may be further impacted by climate change. Climate models considering several emissions scenarios suggest that precipitation levels will likely increase in the coming decades throughout the Missouri River watershed (Kunkel et al. 2013). These models also suggest an increase in the frequency of extreme, heavy precipitation events (Kunkel et al. 2013). How changes in precipitation will influence the hydrology of the Missouri River and its tributaries is less clear, as uncertainty in macro-scale hydrologic modeling can be high (Hagemann et al. 2013). Depending on the general circulation model (GCM) considered, some models predict slight decreases, while others predict slight to significant increases in water yield in the future (Thomson et al. 2005). A U.S. Bureau of Reclamation study, which integrated over 112 GCM projections, predicted that flows will increase by 10–20% in the western portion of the watershed and by >20% in the eastern portion (Alexander et al. 2011). However, to our knowledge, no projections exist for future high-flow return intervals for the Missouri River. In addition, historical observations and future projections indicate high variability and low spatial autocorrelation among sub-basins (U.S. Army Corps of Engineers 2016).

Baseline metapopulation model

Population viability analysis models used in this study were constructed in Vortex (ver10.0.7.3; Lacy et al. 2015). A previously published baseline PVA model for this metapopulation was based on extensive demographic and movement observations from 2008 to 2013 (Catlin et al. 2016). We used this baseline model as the foundation for all model scenarios simulated in this study, and field data and parameters that underlie this model can be found in Catlin et al. (2016).

In the baseline model, movement and demographic rates were specific to each subpopulation, and many of these rates were dependent on the time since a high-flow event last occurred. High-flow events occurred stochastically in the baseline model with a frequency of 5% (i.e., one event approximately every 20 years). Demographic rates and habitat carrying capacities for PLT and LCL in the baseline model were not dependent on the occurrence of high-flow events, because observations showed high flows did not have much, if any, direct impact on these subpopulations. However, immigration rates into these subpopulations from GVP and emigration rates from these subpopulations into GVP were dependent on high-flow events in the model. Habitat within GVP was directly impacted by high flows, and the model was parameterized such that mortality and emigration increased, immigration decreased, and reproduction declined to zero for this population during a high-flow year. In the year after a high-flow event (i.e., the “high-flow+1 year”), the model was parameterized such that the amount of newly created habitat increased, increasing the carrying capacity and attracting an increased number of immigrants. In addition, adult mortality decreased to baseline levels, and hatch year mortality declined to the lowest observed levels. After the high-flow+1 year, immigration/emigration stabilized at baseline levels, and hatch year mortality increased annually until the next high-flow event occurred following a three-year window of low mortality (Hunt 2016). The model was parameterized such that the amount of habitat available to birds in GVP declined each year by a randomly chosen percentage with a uniform distribution spanning 10–60% (U.S. Fish and Wildlife Service 2009) until the next high-flow event occurred, simulating the variable impact of erosion and vegetation encroachment. Additional

details regarding the baseline model can be found in Catlin et al. (2016).

The baseline metapopulation model was simulated for 1000 stochastic replicates of 100 yr to estimate long-term mean values for extinction risk, metapopulation and subpopulation size, and time to extinction. The results showed, given these baseline parameters and assuming the current 20-year high-flow return interval continues, that the metapopulation was unlikely to become extinct under current conditions (0.0 probability of extinction) and would support a population of 203 adults after 100 yr (Table 1; Catlin et al. 2016). The PLT and LCL subpopulations were predicted to have low extinction probabilities (0.0 and 0.003, respectively), supporting populations totaling 123 and 58 adults, respectively, after 100 yr (Table 1; Catlin et al. 2016). The GVP subpopulation had a greater risk of extinction (0.48) and would likely only support approximately 22 adults by year 100 given the current disturbance regime (Table 1; Catlin et al. 2016). For reference, the 2014 population size was estimated at 448 (± 8) breeding adults for the combined LCL and GVP subpopulations (D. H. Catlin, *unpublished data*) and 100–110 adults for the PLT subpopulation (M. Bomberger Brown, *unpublished data*).

We included both demographic and environmental stochasticity in the baseline model. Stochasticity is automatically incorporated by sampling parameters for reproduction (i.e., percentage of males/females breeding, distribution of broods per breeding female) and mortality from binomial distributions governed by the user-given population mean (i.e., the demographic parameter value given) and value for the SD due to environmental variation for each parameter. Additional environmental stochasticity was incorporated by probabilistically modeling high-flow events (or “catastrophes” in Vortex) and by reducing carrying capacity at GVP by a random percentage sampled from a uniform distribution each year. For more information on parameter calculations and their treatment in Vortex, see Catlin et al. (2016) and Lacy et al. (2015).

In the current study, we compared results of scenarios conducted in this study (see next subsection) to those of the baseline model reported in Catlin et al. (2016) to explore how climate change may shift metapopulation extinction risk

Table 1. Scenario results compared to those of the baseline population viability analysis model (Catlin et al. 2016) for a piping plover metapopulation (“Metapop”).

Scenario	High-flow return interval (yr)	Dispersal among populations	Mean population size (number of adults; year 100)				Mean probability of extinction (year 100)			
			PLT	GVP	LCL	Meta-pop	PLT	GVP	LCL	Meta-pop
1. Baseline†	20	Yes	123	22	58	203	0.0	0.48	0.003	0.0
2. Population isolation‡	20	No	122	0	16	138‡	0.002	1.0	0.65	0.002‡
3. Baseline	No high-flow events	Yes	120	0	53	173	0.002	1.0	0.007	0.001
4. Baseline	4§	Yes	124	85	69	277	0.0	0.02	0.001	0.0
5. Baseline	4	No	123	27	16	166‡	0.0	0.75	0.64	0.0‡
6. Dynamic populations¶, local disturbance#	20	Yes	0	0	0	0	1.0	1.0	1.0	0.98
7. Dynamic populations, local disturbance	4	Yes	103	107	106	317	0.12	0.10	0.10	0.07
8. Dynamic populations, global disturbance#	20	Yes	0	0	0	0	1.0	1.0	1.0	1.0
9. Dynamic populations, global disturbance	4	Yes	38	39	43	120	0.60	0.58	0.57	0.53

Note: Populations that comprised the metapopulation included Platte River (PLT), Gavins Point Reach (GVP), and Lewis and Clark Lake (LCL).

† Results according to Catlin et al. (2016).

‡ Population isolation scenario used parameters from the baseline scenario, with the exception that no dispersal was allowed between populations. In table columns for “Metapop” for any scenario where there is no dispersal between populations, the value for mean population size is the sum of the population sizes for individual populations, and the value for mean probability of extinction is the probability that all three populations become extinct in 100 yr in the same model iteration. For these scenarios, a true metapopulation does not exist.

§ For all scenarios listed here where the high-flow return interval (FRI) is <20 yr, the results of this study indicated that the given FRI is the optimal disturbance regime for the conditions modeled in that particular scenario. For example, for scenario 4 above, we found that the optimal FRI for the baseline scenario is 1 flood every 4 years.

¶ In all scenarios with “dynamic populations,” we assumed that all three populations in the metapopulation had carrying capacities as well as mortality, reproduction, immigration, and emigration rates that were affected by the time since a high-flow event last occurred. This is in contrast to the baseline scenario, where high flows affected the demographic and movement rates for piping plovers within GVP only.

In the dynamic populations scenarios, we modeled some scenarios where high-flow events were “local” (i.e., one event affected only one population) and “global” (i.e., events were spatially autocorrelated and affected all populations in the metapopulation).

and abundance from those under the current disturbance regime.

Population viability analysis

In the current study, we simulated scenarios in Vortex for each year post-high-flow event, using dispersal, reproduction, and mortality rates associated with the appropriate number of years since the last high-flow event occurred. From these simulations, we calculated each subpopulation’s deterministic finite rate of increase (λ_{det}) to determine whether populations were sources ($\lambda_{\text{det}} \geq 1$) or sinks ($\lambda_{\text{det}} < 1$; Pulliam 1988). In Vortex, λ_{det} is calculated from a life table analysis of the mean reproduction and survival rates used in the model and does not take into account immigration or emigration (Lacy et al. 2015).

We then simulated a series of PVA scenarios in which we used baseline metapopulation parameter

values for all parameters except where noted. Because of high uncertainty in hydrologic projections (Hagemann et al. 2013), we conducted “a broad exploration of novel futures,” as recommended by Seidl et al. (2016). These scenarios included:

1. Population isolation scenario: We assumed that subpopulations do not form a metapopulation, and we prohibited dispersal between all pairs of subpopulations. This scenario simulated the viability of subpopulations if habitat supporting the other subpopulations in the metapopulation were destroyed through, for example, land-use change not related to dams. Given the small size of subpopulations and that birds in PLT primarily use human-maintained habitats, there is a strong chance that the metapopulation could

be reduced to a single population in the future.

2. High-flow regime scenarios: We simulated 24 scenarios in which we considered the baseline metapopulation structure but (1) assumed high-flow events never occurred, (2) varied the high-flow return interval in one-year increments from 1 to 20 yr, and (3) varied the high-flow return interval in 10-year increments from 20 to 40 yr. These scenarios allowed us to (1) understand viability and abundance today under a suppressed disturbance regime compared to those under a more historical regime and (2) evaluate the effects of climate-driven alterations to the disturbance regime, should climate alterations directly or indirectly increase or decrease high-flow return intervals. Given historical water management trends and climate change projections, it is most likely that the frequency of high-flow events will remain the same or increase.
3. Dynamic metapopulation scenarios: We simulated a hypothetical metapopulation under “historical” conditions where all three subpopulations exhibit immigration, emigration, mortality, and reproduction rates that are a function of the time since a high-flow event last occurred. Results of these scenarios provided a contrast to viability under current, disturbance-suppressed conditions, where high flows only impact GVP. We simulated models where high-flow events were local (i.e., only one subpopulation was affected per high-flow event) or global (i.e., all subpopulations were simultaneously affected by a single high-flow event), and we varied the high-flow return interval in one-year increments from 0 to 20 yr. Global scenarios also allowed us to simulate the effects of climate-driven changes to the disturbance regime, where much larger extreme weather events than currently observed affect habitat for all three populations simultaneously. Although more extreme weather events are likely in the future, it is possible but unlikely that a single disturbance would impact all subpopulations simultaneously based on the size of past high-flow events and a projected lack of autocorrelation in future events (Alexander et al. 2011).

All models were simulated for 1000 stochastic replicates of 100 yr to estimate mean values for extinction risk and population size.

Sensitivity analysis

Given the uncertainty in some parameters (e.g., percentage of adult females breeding) and the anticipated importance of others (e.g., frequency of high flows, rate of decline in carrying capacity), we conducted a sensitivity analysis for select parameters used in the baseline metapopulation model. We considered the rate of habitat loss, difference in dispersal rates between hatch year birds and adults, percentage of females breeding, frequency of high-flow events, emigration from GVP during a high-flow year, immigration into GVP in a high-flow+1 year, habitat carrying capacity for all three subpopulations, and adult mortality at GVP during a high-flow year. We did not systematically analyze other mortality and reproduction rates, because previous studies have shown that models are sensitive to adult and juvenile mortality (e.g., Calvert et al. 2006, Brault 2007).

We conducted sensitivity analysis sensu McCarthy et al. (1995). Using Vortex, we generated 500 parameter sets for the parameters listed above, allowing the program to randomly choose a value from a uniform distribution within a user-specified range for each parameter considered (Latin hypercube sampling; Table 2). The program simulated 500 stochastic replicates for each parameter set (keeping all other parameters in the model at baseline values) to produce 250,000 binary observations of population persistence or extinction by year 100. Using the parameter set values as independent variables and whether the population went extinct by year 100 as the binary dependent variable, we conducted logistic regression using R (R Development Core Team 2014) and compared the standardized regression coefficients to rank the importance of each independent variable in relation to extinction risk. A higher absolute value for a standardized regression coefficient indicates a higher level of model sensitivity for that parameter, and the relative importance of each parameter is reflected in the relative magnitude of the standardized regression coefficient (McCarthy et al. 1995).

Table 2. Structure and results of the sensitivity analysis for select parameters used within the baseline population viability analysis model for the piping plover metapopulation.

Parameter	Baseline value	Min value	Max value	Standardized coefficients (z-values)			
				Metapop	PLT	GVP	LCL
Females breeding (%)	100	75	100	-140.5	-143.5	-108.5	-167.6
PLT habitat carrying capacity (number of individuals)	135	75	180	-67.7	-68.8	-50.3	-106.8
Annual % of habitat loss for GVP in the absence of high flows (% of current carrying capacity)	35	10	80	55.2	51.3	188.0	116.8
Frequency of high flows† (annual probability)	5	1	25	-30.0	-27.0	-170.6	-89.8
GVP carrying capacity in a high-flow+1 year (number of individuals)	2154	1000	3000	-7.7	-7.5	-8.5	-11.5
LCL habitat carrying capacity (number of individuals)	98	50	150	-6.8	-6.9	-9.5	-7.7
Dispersal modifier (ratio of hatch year to adult dispersal rates)	2.3	1	2	4.3	4.7	2.3	7.0
Dispersal from GVP to PLT in a high-flow year	5.9	1.6	10	-3.7	-4.5	2.1	-0.4
Dispersal from PLT to GVP in a high-flow+1 year	4.1	1.7	6	2.5	3.4	-16.4	-5.9
Dispersal from GVP to LCL in a high-flow year	31.5	8.4	40	1.587	2.213	4.674	-0.737
Adult mortality for GVP in a high-flow year (%)	35.5	27.3	40	1.568	1.380	9.854	9.359
Dispersal from LCL to GVP in a high-flow+1 year	20.4	7.8	30	0.926	0.065	3.376	7.984

Note: The metapopulation ("Metapop") consisted of subpopulations on the Platte River (PLT) and on the Missouri River at Gavins Point Reach (GVP) and Lewis and Clark Lake (LCL).

† Although the demographic rates for piping plovers within PLT and LCL were not directly affected by high-flow events, these populations were indirectly affected through changes in GVP's immigration and emigration rates during and following high-flow events.

RESULTS

The λ_{det} values revealed that both PLT and LCL were consistently source populations irrespective of disturbance frequency, with values of 1.15 and 1.02, respectively (Fig. 2). GVP's role as a source or sink varied depending on how long it had been since a high-flow event last occurred. During a high-flow year, when productivity and survival were at their lowest levels, λ_{det} approached 0, and the population was a strong sink. From the high-flow+1 year to 15 years post-event, the population was a source ($\lambda_{\text{det}} = 1.27$ to 1.00), with reproduction exceeding mortality. The population was a sink from 16 years post-event until the next high flow occurred ($\lambda_{\text{det}} \leq 0.98$; Fig. 2).

The metapopulation's extinction probability was highly sensitive to the population's percentage of females breeding (negative correlation) followed by PLT's habitat carrying capacity (positive correlation) and GVP's annual rate of habitat loss due to erosion and vegetation encroachment (negative correlation; Table 2). Extinction risk was moderately sensitive (i.e., relative to other parameters considered) to the frequency of high-flow events and was comparatively insensitive to the remaining parameters tested (Table 2).

Predictions for population size and extinction risk were substantially affected by both the metapopulation structure and the disturbance regime. Isolated populations (i.e., in the population isolation scenario) with a 20-year high-flow return interval supported fewer adults by year 100, while GVP and LCL had substantially higher risks of extirpation compared to the results of the baseline metapopulation model (Table 1). The metapopulation supported the highest number of adults and had the lowest extinction risk at 277 adults and 0.0, respectively, when subpopulations were linked through dispersal and when high flows occurred every 4 years (Table 1, Fig. 3). The predicted population size declined, however, when high flows occurred more often than every 4 years (Fig. 3). The predicted population size also declined when high-flow events occurred less frequently than every 4 years (Fig. 3).

When we assumed all populations in the metapopulation were dynamic, where carrying capacity, mortality, reproduction, and immigration/emigration were related to the time since a high-flow event occurred for all populations, we found the metapopulation could not persist over longer (i.e., ≥ 15 -year intervals) high-flow return intervals (Fig. 4). Assuming high-flow events were localized (i.e., a high-flow event only impacted

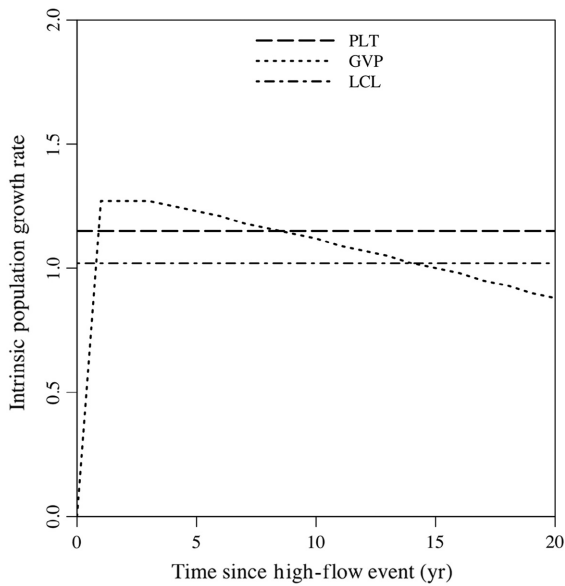


Fig. 2. Deterministic intrinsic rates of population growth (λ_{det}) for piping plover populations at Gavins Point Reach (GVP), Lewis and Clark Lake (LCL), and Platte River (PLT). Values were calculated from parameters used in the baseline population viability analysis metapopulation model, based on observations of the populations from 2008 to 2013 (Catlin et al. 2016). λ_{det} values ≥ 1 are indicative of a stable or growing source population, and values < 1 are indicative of a declining sink population. The λ_{det} values for GVP drop below 1 at 15 years post-high-flow event, suggesting that this population becomes a sink when a high-flow event has not occurred in 16 or more years.

one subpopulation), the metapopulation had a 0.99 probability of extinction in 100 yr under the current disturbance regime (i.e., high-flow return interval of 20 yr; Table 2, Fig. 4). In this scenario, metapopulation size was optimized at a four-year high-flow return interval. At this return interval, the dynamic metapopulation had a 0.07 probability of extinction and could support a larger total population size at 317 adults compared to the more static baseline metapopulation (277 adults at an optimal four-year return interval; Table 2, Fig. 4). A dynamic metapopulation was more likely to persist when high flows were localized (Table 2, Fig. 4); a metapopulation in which one high-flow event affected all subpopulations simultaneously had a 0.53 probability of extinction and supported a total population of 120 adults even at its optimal return interval of 4 yr.

DISCUSSION

Piping plover metapopulation dynamics on the Missouri and Platte rivers, under both current and possible future scenarios, provide empirical support for several important theoretical concepts relating to species in dynamic habitats:

1. Species in dynamic environments are more at risk from habitat loss (Wimberly 2006, North and Ovaskainen 2007, Martin and Fahrig 2016) and require larger quantities of suitable habitat (Johst et al. 2011) than species inhabiting landscapes with minimal habitat turnover.

High-flow events are the natural habitat creation mechanisms on the Missouri, Platte, and many other large floodplain rivers, and habitat is lost quickly to erosion and vegetation encroachment without these events. Therefore, suppression of the disturbance regime equates to a loss of habitat for piping plovers and other disturbance-dependent species in the system. Piping plovers exhibit several adaptations to the historical disturbance regime in the Great Plains by (1) laying

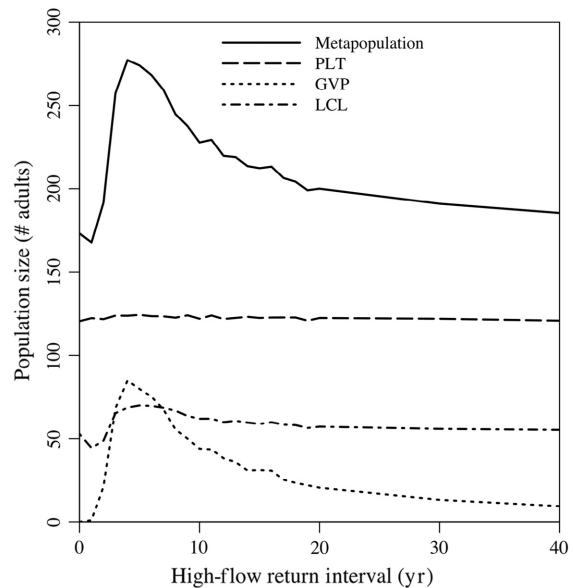


Fig. 3. Population size at year 100 for individual subpopulations at Gavins Point Reach (GVP), Lewis and Clark Lake (LCL), and Platte River (PLT) and for the entire metapopulation as a function of the high-flow return interval.

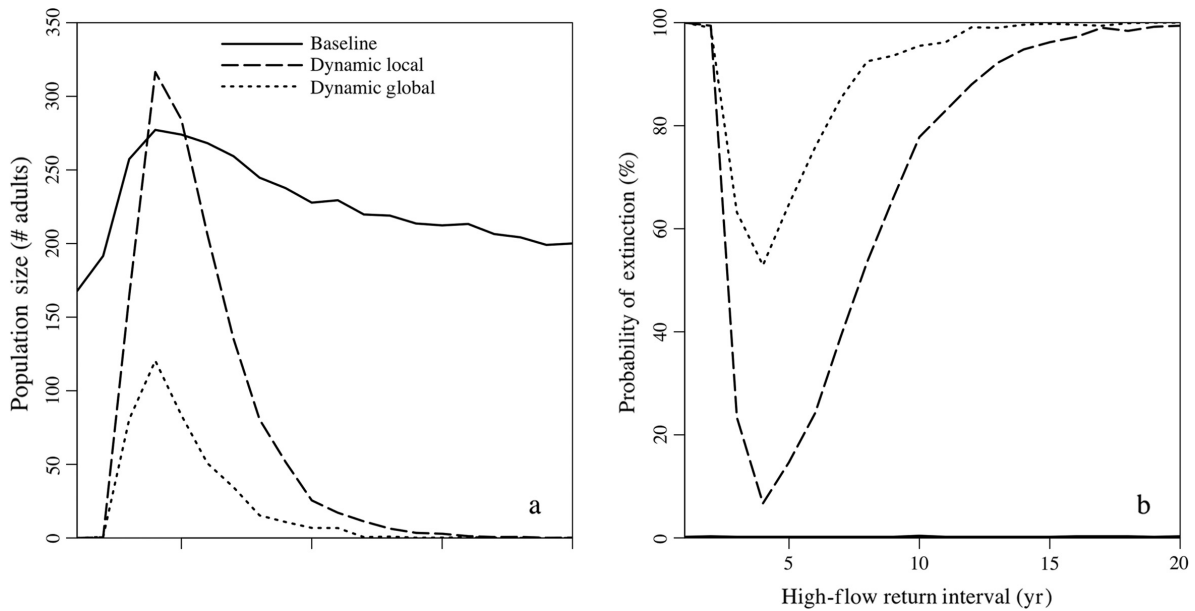


Fig. 4. (a) Total population size at model year 100 and (b) the probability of extinction for the Missouri–Platte River piping plover metapopulation based on population viability analysis scenarios that assume (1) current metapopulation structure and disturbance effects (i.e., baseline model conditions; “baseline”), (2) a metapopulation where component populations are dynamic and where disturbances are not spatially autocorrelated (“dynamic local”), and (3) a metapopulation where component populations are dynamic and where disturbances are spatially autocorrelated (“dynamic global”). In these dynamic population scenarios, the habitat carrying capacities and mortality, reproduction, and dispersal rates for all three populations are affected by the time since a high flow last occurred. This is in contrast with the baseline scenario, where demographic and movement rates are affected by the time since a high flow last occurred for the Gavins Point Reach population only. Note: Baseline probability of extinction is 0.0 and falls along the x -axis in b.

eggs in mid- to late May immediately following historical spring high-flow peaks (Catlin et al. 2010), (2) renesting up to four times in a breeding season in the event that eggs or hatchlings are lost to flooding (U.S. Fish and Wildlife Service 2000), (3) compensating for high mortality and low reproduction in a high-flow year with high reproduction and recruitment in years following those disturbances (Catlin et al. 2016), and (4) increasing dispersal rates and distances during high-flow years (Catlin et al. 2016). Such life history adaptations are expected for species in dynamic environments where disturbances are frequent, large, and predictable (Lytle and Poff 2004), characteristic of the historical Missouri and Platte rivers (Hesse and Mestle 1993). As observed in other species adapted to a specific disturbance regime (Kelly et al. 2014, Ranius et al. 2014, McElderry et al. 2015, Paniw et al. 2015), we found that the piping plover metapopulation supported fewer

adults (74 adults) and that the GVP subpopulation had a higher risk of extinction (+0.45) under a suppressed disturbance regime compared to a more natural four-year high-flow return interval under which this species adapted. In addition, a metapopulation that was fully dynamic, where habitat availability was dependent on the disturbance regime for all three subpopulations in the metapopulation, would have a near-certain risk of extinction under the current, suppressed disturbance regime.

Furthermore, the only subpopulation with habitat not artificially maintained, GVP, had a 0.48–1.0 probability of extinction at high-flow return intervals ≥ 20 yr. An important critical threshold for persistence (Keymer et al. 2000) in this dynamic subpopulation exists where high-flow events occur at ≤ 15 -year intervals; at this threshold, the subpopulation acted as a source instead of a sink.

Sensitivity results also lend credence to the hypothesis that species in dynamic landscapes are especially vulnerable to habitat loss. Metapopulation persistence was most sensitive to parameters that were related to habitat loss: percentage of females breeding (partially a function of carrying capacity) and, to a lesser extent, PLT's carrying capacity, the rate of habitat loss at GVP, and the frequency of high-flow events. Similarly, the persistence of GVP was even more sensitive to these parameters, as exemplified in the higher magnitudes of the standardized regression coefficients.

Climate change can affect habitat availability for disturbance-dependent species by influencing disturbance regimes in dynamic landscapes (e.g., Serra-Diaz et al. 2015). Although there is high uncertainty in hydrologic projections for rivers worldwide (Hagemann et al. 2013), including the Missouri and Platte rivers (Thomson et al. 2005), the general consensus is that the frequency of high-flow events will increase under a changing climate in the Great Plains (Alexander et al. 2011). Therefore, in this region, climate change will most likely revert the disturbance regime from a 20-year high-flow return interval in the direction of more historical patterns to the benefit of piping plovers. Climate change would have the greatest positive impacts on the metapopulation if increased precipitation allows for high-flow events at ≤ 15 -year return intervals, with the highest metapopulation abundance occurring at a four-year return interval. High variability in model predictions (Hagemann et al. 2013, Wuebbles et al. 2014) and inconsistencies in trends over the past 30 years (Fassnacht et al. 2016), however, make predicting more specific future frequencies in high-flow events difficult.

In addition, climate models suggest that increased temperatures will reduce spring snow-melt peaks but increase winter flows in the Great Plains (Wuebbles and Hayhoe 2004). By reducing reproduction to 0 for GVP in high-flow years, we modeled high flows as events like that of the 2010/2011 flood that occurs during the late spring/summer months. Therefore, piping plovers could benefit even more from climate change if high flows occur in winter months, producing habitat but not hindering reproduction (Catlin et al. 2010, 2015).

If there is an increased frequency of droughts or decreases in stream-flow in this region, which

is unlikely but possible according to some climate change scenarios (Thomson et al. 2005), climate change will continue to push the disturbance regime farther from historical patterns. Under this scenario, the risk of extirpation for the GVP subpopulation approaches certainty, and the persistence of the metapopulation will be largely due to the persistence of human-maintained plagioclimax habitats at LCL and PLT. In general, changes outside the natural range of disturbance, temperature, precipitation, or other environmental factors will likely have drastic consequences for ecosystem structure depending on the rate of those changes and a species' adaptive capacity (Poff et al. 2002). Land-use change and management can exacerbate climate change-related alterations to disturbance regimes, causing "resource bottlenecks" that have led to population crashes and extinctions for several species (Maron et al. 2015).

2. Species in dynamic habitats are also vulnerable to a loss in habitat connectivity (Johst et al. 2011).

A loss of connectivity in this metapopulation greatly increased the risk of extirpation of two (LCL and GVP) of the three subpopulations, regardless of the frequency of high-flow events. The risk of extirpation for LCL rose from 0.003 to 0.65 and from 0.004 to 0.64 under 20-year and four-year high-flow return intervals, respectively, when emigration from neighboring subpopulations was prohibited. Similarly, GVP's risk of extirpation increased from 0.48 to 1.0 under a 20-year high-flow return interval and from 0.02 to 0.75 under a four-year return interval. Connectivity among habitat patches and subpopulations in dynamic landscapes allows individuals to escape from areas of habitat destruction and to (re)colonize newly created or improved habitats (Johst et al. 2011). In this metapopulation, connectivity to the source populations at PLT and LCL also likely improved the persistence of GVP through rescue effects (Brown and Kodric-Brown 1977).

3. Persistence of species in dynamic habitats may be optimized at intermediate disturbance regimes (Wimberly 2006) with non-spatially autocorrelated disturbances (Kallimanis et al. 2005, Vuilleumier et al. 2007).

Peak metapopulation persistence and abundance occurred when high-flow events of the magnitude observed in 2010/2011 occurred every 4 years, both when only GVP experienced habitat turnover (baseline metapopulation scenarios) and when all three subpopulations experienced habitat turnover (dynamic population scenarios). Metapopulation extinction risk and abundance declined most rapidly when high flows occurred more frequently than every 4 years. In the unlikely event that climate change increases the frequency of high flows beyond this threshold, the climate-driven disturbance regime could exceed the metapopulation's ability to recover from disturbances, as seen in other systems (Swab et al. 2012, Penman et al. 2015).

Our results also highlight more complex relationships between climate and disturbance in this region if larger, more extreme, spatially autocorrelated high-flow events begin to destabilize habitats used by PLT and LCL simultaneously. When we assumed high-flow events influenced the demography and movement of all subpopulations but were local in nature (i.e., a high-flow event only affected one subpopulation at a time, no spatial autocorrelation in disturbance), metapopulation extinction risk was higher and abundance was lower compared to the baseline model. The only exception to these trends occurred at four- and five-year high-flow return intervals, where abundance for the fully dynamic metapopulation was predicted to be higher than that of the baseline model at equivalent high-flow return intervals. When high-flow events were global in nature (i.e., one event affected all three subpopulations simultaneously, spatial autocorrelation in disturbance), metapopulation extinction risk was always substantially higher and abundance lower compared to local dynamic and baseline scenarios. As in any metapopulation, regional stochasticity can lead to spatially correlated population dynamics that ultimately reduce the likelihood of metapopulation persistence (Hanski 1998). When disturbances are spatially autocorrelated in dynamic landscapes, particularly at low disturbance frequencies, a large proportion of habitat can be simultaneously rendered unsuitable and cause metapopulation extirpation (e.g., Stelter et al. 1997). In a novel future, the focal piping plover metapopulation would likely be extirpated if rare single, very

extreme high-flow events affected the entire metapopulation, particularly if such events occur within an otherwise suppressed (i.e., high-flow return interval ≥ 20 yr) disturbance regime.

Conservation implications

A suppressed disturbance regime on the Missouri and Platte rivers increased the extirpation risk of component piping plover subpopulations and decreased the functional carrying capacity of the metapopulation. Climate change could reduce extinction risk and improve abundance by increasing the frequency of high-flow disturbances, ultimately increasing habitat availability. This beneficial climate change effect, however, depends on the interplay between climate change and land-use policies in this and other disturbance-dependent landscapes (e.g., Regos et al. 2015). With reduced mountain snowpack, reduced summer precipitation, and higher temperatures, droughts and reduced summer flows are also a possibility in the Great Plains and Midwestern United States (Wuebbles and Hayhoe 2004, Chien et al. 2013). Our research indicates that, should managing entities limit winter flows in an effort to store water in reservoirs for summer use, this piping plover metapopulation could be negatively affected in several ways. Despite higher winter precipitation levels, many high-flow events that would otherwise create habitat on the river could be suppressed and released later in the summer. Our models show that piping plover metapopulation abundance and viability would continue to decline from present levels if the high-flow return interval is further suppressed. In addition, an increased storage of water in Lewis and Clark Lake for later summer use could submerge some of the sandbar habitat used by the LCL subpopulation, reducing the already small carrying capacity of that subpopulation and overall metapopulation capacity. Finally, artificial high summer flows are generally harmful to piping plover reproduction and recruitment (Catlin et al. 2013, 2014).

Under the current suppressed flow regime, the consistent presence of early-successional habitat (i.e., plagioclimax habitat) able to support even a small source subpopulation (like PLT) as well as connectivity among subpopulations was necessary for the persistence of the metapopulation. Plagioclimax habitat that supports PLT is maintained through mining operations, and this

source population acted as a stabilizing buffer regardless of the high-flow return interval. Some man-made disturbances and the habitats they create may become important refugia for early-successional species, as also observed for the pyrophytic dewy pine (*Drosophyllum lusitanicum*) in a fire-suppressed Mediterranean heathland (Paniw et al. 2015).

We conclude that climate change could have positive effects on disturbance-dependent species in ecosystems where disturbances have been anthropogenically suppressed when climatic shifts move disturbance regimes toward more historical patterns. However, this benefit will only be realized if land-use management policies do not counteract expected benefits. Furthermore, stable source populations, even if unintentionally maintained through anthropogenic activities, may be critical for the persistence of metapopulations of early-successional species under both suppressed disturbance regimes and disturbance regimes where climate change has further altered disturbance frequency or scope.

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