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Contributed Paper

Application of multiple-population viability analysis to evaluate species recovery alternatives

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Abstract: Population viability analysis (PVA) is a powerful conservation tool, but it remains impractical for many species, particularly species with multiple, broadly distributed populations for which collecting suitable data can be challenging. A recently developed method of multiple-population viability analysis (MPVA), however, addresses many limitations of traditional PVA. We built on previous development of MPVA for Lahontan cutthroat trout (LCT) (*Oncorhynchus clarkii henshawi*), a species listed under the U.S. Endangered Species Act, that is distributed broadly across habitat fragments in the Great Basin (U.S.A.). We simulated potential management scenarios and assessed their effects on population sizes and extinction risks in 211 streams, where LCT exist or may be reintroduced. Conservation populations (those managed for recovery) tended to have lower extinction risks than nonconservation populations (mean = 19.8% vs. 52.7%), but not always. Active management or reprioritization may be warranted in some cases. Eliminating non-native trout had a strong positive effect on overall carrying capacities for LCT populations but often did not translate into lower extinction risks unless simulations also reduced associated stochasticity (to the mean for populations without non-native trout). Sixty fish or 5–10 fish/km was the minimum reintroduction number and density, respectively, that provided near-maximum reintroduction success. This modeling framework provided crucial insights and empirical justification for conservation planning and specific adaptive management actions for this threatened species. More broadly, MPVA is applicable to a wide range of species exhibiting geographic rarity and limited availability of abundance data and greatly extends the potential use of empirical PVA for conservation assessment and planning.

Keywords: conservation planning, decision-support tools, endangered, extinction risk, hierarchical Bayesian model, recovery planning, threatened

Aplicación de un Análisis de Viabilidad Multi-Poblacional para Evaluar Alternativas de Recuperación de Especies

Resumen: El análisis de viabilidad poblacional (AVP) es una herramienta poderosa de conservación, que desafortunadamente sigue siendo impráctica para muchas especies, en particular para aquellas con poblaciones múltiples distribuidas ampliamente, para las cuales puede ser un reto la recolección de datos apropiados. Sin embargo, un método recientemente desarrollado de análisis de viabilidad multi-poblacional (AVMP) aborda muchas de las limitaciones de los AVP tradicionales. Partimos del desarrollo previo de un AVMP para la trucha degollada lahontana (LCT, en inglés) (*Oncorhynchus clarkii henshawi*), una especie enlistada bajo el Acta de Especies en Peligro de los Estados Unidos, la cual está distribuida ampliamente a lo largo de los fragmentos de hábitat que se

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encuentran en la Gran Cuenca (E.U.A.). Simulamos los escenarios potenciales de manejo y evaluamos sus efectos sobre el tamaño de las poblaciones y los riesgos de extinción en 211 arroyos en donde existe la LCT o en donde podría ser reintroducida. Las poblaciones de conservación (aquellas manejadas para su recuperación) tuvieron una tendencia hacia un riesgo de extinción más bajo que las poblaciones sin conservación (media = 19.8% vs. 52.7%), pero no en todos los casos. El manejo activo o la repriorización podrían ser justificadas en algunos casos. La eliminación de las truchas no nativas tuvo un fuerte efecto positivo generalizado sobre las capacidades de carga de las poblaciones de LCT, aunque frecuentemente esto no se transformó en un riesgo de extinción más bajo a menos que las simulaciones también redujeran la estocasticidad asociada (para la media de las poblaciones sin truchas no nativas). Para proporcionar un éxito de reintroducción cercano al máximo, el número mínimo de reintroducción debió ser de 60 peces o una densidad de 5–10 peces/km. Este marco de trabajo para el modelo proporcionó una percepción muy importante y una justificación empírica para la planeación de la conservación y para las acciones de manejo adaptativo para esta especie amenazada. En términos más generales, el AVMP puede aplicarse a una gama amplia de especies que exhiban una rareza geográfica y una disponibilidad limitada de datos de abundancia, además de que expande enormemente el uso potencial de AVP empíricos para la evaluación y planeación de la conservación.

Palabras Clave: amenazada, en peligro, herramientas de apoyo de decisiones, modelo bayesiano jerárquico, planeación de la conservación, planeación de la recuperación

摘要: 种群生存力分析是一项强大的研究保护的工具, 但在许多物种中尚不能实际应用, 特别是那些由于种群多、分布广而难以收集合适数据的物种。不过, 近期发展起来的多种群生存力分析方法则能解决传统的种群生存力分析存在的许多局限性。我们在之前的基础上对拉洪坦切喉鳟 (*Oncorhynchus clarkii henshawi),* 一种在美国大盆地栖息地碎片中广泛分布, 并被列入《美国濒危物种法案》的物种, 进行了多种群生存力分析。我们模拟了多种可能的管理情景, 并评估了211条存在原生或重引入的拉洪坦切喉鳟的河流中这些管理情景对种群大小和灭绝风险的影响。结果表明, 保护种群 (为恢复进行管理的种群) 的灭绝风险要低于非保护种群 (均值分别为19.8% 和52.7%), 但也并非绝对如此。在某些情况下, 可能需要积极管理或重新确定保护优先级。清除外来鳟鱼对拉洪坦切喉鳟种群的总体承载力有积极影响, 但这通常不直接等同于降低灭绝风险, 除非在模拟中同时减少相关随机性 (清除外来鳟鱼后的种群数量均值) 。而当重引入的最低数量或密度分别为60条鱼或每公里5-10条鱼时, 可以使重引入成功率接近最高。这个模型框架为该濒危物种的保护规划和具体的适应性管理行动提供了重要的见解和经验依据。在更广泛的层面上看, 多种群生存力分析还适用于地理上稀有、丰度数据有限的许多物种, 大大扩展了种群生存力分析在保护评估和规划中的应用前景。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 受胁迫, 濒危, 灭绝风险, 保护规划, 恢复规划, 决策支持工具, 层次贝叶斯模型

Introduction

Population viability analysis (PVA) is a modeling framework for exploring factors influencing population dynamics and extinction risk over a given time frame. Although a powerful conservation tool that can be used both to inform theory and prioritize specific conservation actions (Beissinger & McCullough 2002), PVA is not always feasible to apply due to intensive data requirements (Ralls et al. 2002; Reed et al. 2002; Wolf et al. 2015). This is particularly true for species occurring in multiple populations, each of which requires a separate PVA. Recent development of multiple population viability analysis (MPVA) (Wenger et al. 2017) offers an alternative that can address this limitation. This approach models abundance and dynamics at multiple locations simultaneously, drawing on information from more data-rich populations to make inferences for data-poor populations (Wenger et al. 2017). More recently, this process model was integrated into a Bayesian hierarchical framework incorporating an observation and a sampling model to account for additional sources of uncertainty (i.e., imperfect detection and sampling error) (Leasure et al. 2018).

Via application to a trout native to the interior western United States, we used hierarchical MPVA to evaluate recovery-action alternatives for a widely dispersed but locally rare species of conservation concern. The Lahontan cutthroat trout (LCT) (*Oncorhynchus clarkii henshawi*) is distributed across the remote geography of the northwestern Great Basin (U.S.A.) (Fig. 1), but its habitat is highly fragmented (Dunham et al. 1997) and the species is listed as threatened under the U.S. Endangered Species Act (Coffin & Cowan 1995; USFWS 2009). Management primarily involves efforts to remove non-native trout (a principal threat) (USFWS 2009) and reintroduce LCT to habitat throughout its historical range. Although commonly advocated for species of conservation concern, control of non-native species and reintroductions are expensive, long-term investments with uncertain benefits (Cochran-Biederman et al. 2015; Dunham et al. 2016). Accordingly, the application of a data-driven modeling framework that estimates the relative probability of success of these actions across multiple populations can generate crucial insights and empirical justification for identifying and prioritizing effective conservation actions (e.g., Doak et al. 2015; Evans et al. 2016).

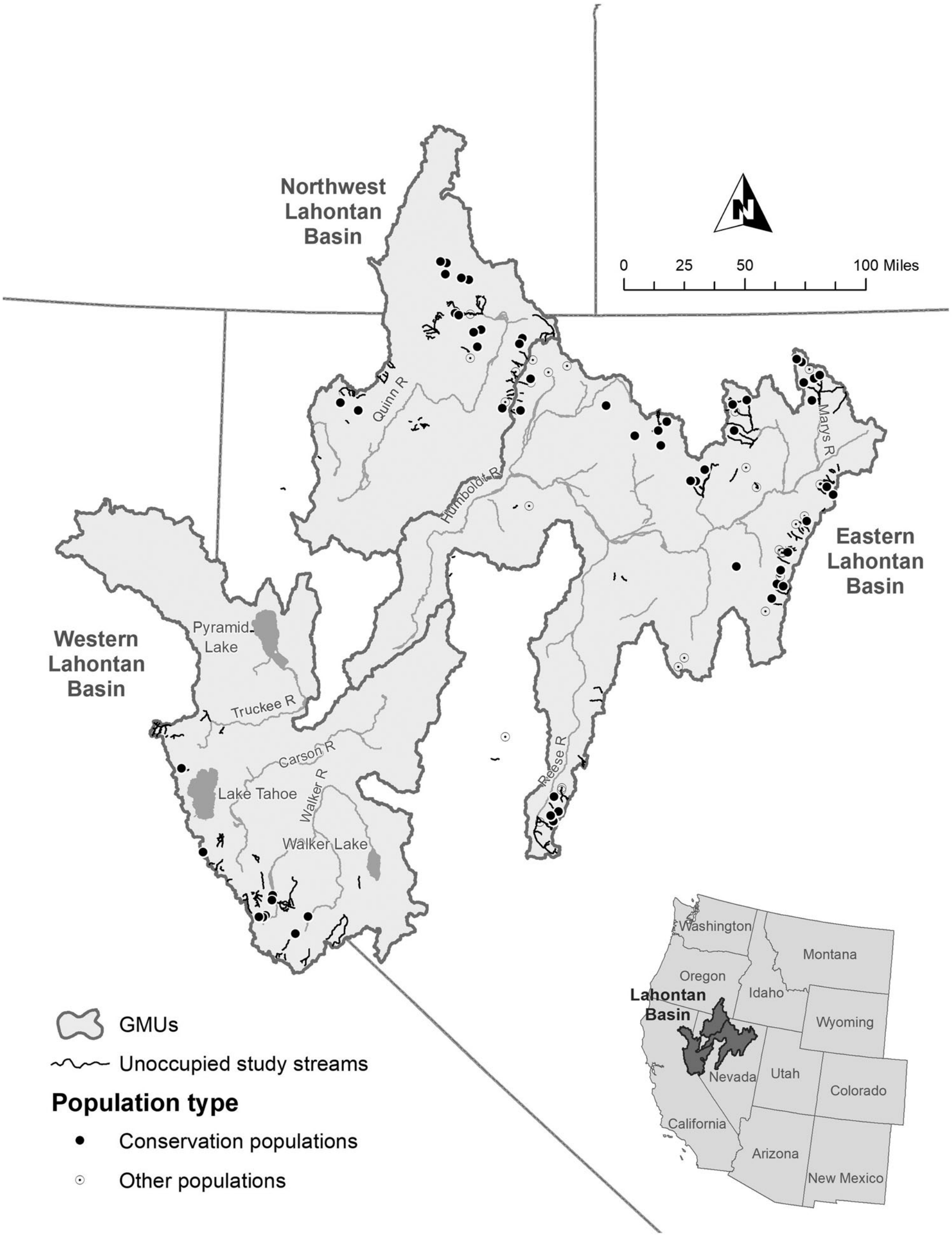

Figure 1. Map of the historical range of Lahontan cutthroat trout shown relative to 3 major geographic management units (western, northwestern, and eastern basins). Unoccupied streams are evaluated for probability of successful reintroduction.

Using parameter estimates from a previously developed MPVA for LCT (Leasure et al. 2018), we simulated management scenarios and assessed their effects on population sizes and extinction risks in 211 streams, where LCT exist or may be reintroduced. Specifically, we applied MPVA to rank extinction risk for current populations range wide; estimate the benefit of removing non-native trout from relevant populations; and determine the viability of LCT reintroduced to unoccupied historical waters under different scenarios. Although our application focused on a trout, our findings highlight the new capabilities MPVA offers to managers of a wide range of species characterized by geographic rarity and limited abundance data.

Methods

Study Area and Stream Delineation

Our study area encompassed the historical range of LCT in the northern Great Basin Desert (Fig. 1). We assessed all populations from the Lahontan MPVA (Leasure et al. 2018) plus 56 streams within the fish's historical range, where the likelihood of reintroduction success could be evaluated. Collectively, these included 84 streams, where LCT had been observed by management agencies (occupied streams) and 127 historical streams, where LCT had not been observed in the last several decades (unoccupied streams). Occupied streams included 57 conservation populations identified for recovery based largely on genetic integrity and assumed resiliency (Coffin & Cowan 1995; USFWS 2009). Unoccupied streams were assumed to contain LCT habitat because they currently support non-native trout populations (the likely cause of LCT extirpation) or were selected by management partners based on habitat data or resolved historical threats. Except for several previously transplanted populations of conservation interest, we did not include populations outside the historical range of LCT. We also omitted the 2 remaining populations with a lacustrine (lake) migratory component because our current model framework does not accommodate this habitat and biological complexity. Data were counts of age 1 or older LCT captured during backpack electrofishing surveys from 1985 to 2016 (details are given in Leasure et al. [2018]). This encompassed 15,265 LCT captured during 3967 field surveys over 271 km of electrofishing.

As in Leasure et al. (2018), we extracted spatial extents of conservation populations from the most recent range-wide status assessment (USFWS 2009). For other occupied streams, we used elevation contours to estimate upstream and downstream LCT distribution limits (Warren et al. 2014). Occasionally, we modified extents based on historical field sampling data and the presence of barriers identified by agency staff and 2 existing databases (U.S. Fish and Wildlife Service LCT range-wide and Humboldt-Alvord assessments). We included barriers classified as culvert, fish-management barrier, dam, water diversion, or waterfall (1.8 m or higher). We excluded those classified as beaver dam or velocity barrier. If a barrier occurred within the extent of a population, we divided the population into 2 demographically closed populations. Final delineations were reviewed and confirmed by agency partners.

MPVA Model Application

The Lahontan MPVA modeled density-dependent population dynamics via a process model (Wenger et al. 2017) linked to a sampling and an observation model (details of this hierarchical structure are given in Leasure et al. [2018]). We focused on application of the process model (a single level of the full hierarchical model) to estimate population dynamics as a function of environmental covariates measured annually from 1985 to 2016 across the entire subspecies distribution. Mean August stream temperature was estimated with the NorWeST model (Isaak et al. 2017). Warmer stream temperatures had a significantly negative effect on population growth rates (Leasure et al. 2018). Peak annual stream flows were estimated by the variable infiltration capacity model in NASA's National Land Data Assimilation Systems (Xia et al. 2012). We chose this metric based on its previously observed influence on western trout distributions (Wenger et al. 2011*b*) and relative accuracy compared with other modeled flow metrics (e.g., summer low-flows) (Wenger et al. 2010; Wenger et al. 2011*a*). Higher peak flows had a weak positive effect on population growth rates (Leasure et al. 2018). Riparian vegetation was assessed by the satellite-based normalized difference vegetation index (NDVI) (Pettorelli et al. 2011) calculated from Landsat images with the Google Earth engine (Gorelick et al. 2017); NDVI does not detectably effect LCT carrying capacities (Leasure et al. 2018).

We created an index of non-native trout density from count data provided by agency partners because these data lacked sufficient collection consistency and detail to permit estimation of detection probabilities or sampling error. To calculate the index, we summed non-native counts among all sampled sites and divided this by the total length of sampled stream reaches. Sampling of non-native trout was not always performed annually. For streams with only 0s observed for years with data (i.e., an apparent lack of non-native trout), we consulted LCT biologists to confirm the appropriateness of filling in missing years with 0s. For other streams, we used a moving weighted-average density for years without data. Non-native trout densities have a significant negative effect on LCT carrying capacities (i.e., an increase in the strength of density dependence) (Leasure et al. 2018).

We forecast population dynamics over 30 years, assembling a covariate time series to represent future conditions, assumed to resemble historical conditions, by resampling from historical covariate time series (1985–2016) in each population. A historical year was selected at random (with replacement) and covariate values from that year were used to represent a future year. This was repeated for each year in the forecast period to assemble a complete 30-year time series. We then repeated the process to create 100 replicate time series that differed randomly in the sequence of years.

The Lahontan MPVA included a residual environmental stochasticity parameter (hereafter environmental stochasticity) to account for random variations in population sizes not explained by modeled covariates. This residual variation could represent truly random variation or effects of unassessed environmental factors, such as wildfires, water quality, or stream drying (e.g., Schultz et al. 2017). As for conventional PVA, environmental stochasticity is strongly correlated with population extinction probability (Mangel & Tier 1994) (detailed discussion is given in Supporting Information). We characterized environmental stochasticity for each population (hierarchically, by drawing from a global distribution with hyperparameters) and for the global distribution of values among all populations with data to enable predictions for unoccupied streams or those where field surveys had not been conducted. To evaluate how estimates were affected by the use of available covariates, for occupied streams we compared population forecasts that used population-specific estimates with those based on the global estimate of environmental stochasticity.

The MPVA forecast procedure was a multistep process. For each year (t) in each population (i), forecast covariates were used to estimate an intrinsic population growth rate (r) and the effect of density-dependence (ϕ) for a population:

$$r_{i,t} = \beta_0 + \beta_1 x_{1,i,t} + \beta_2 x_{2,i,t}$$

and

$$\phi_{i,t} = \alpha_0 + \alpha_1 z_{1,i,t} + \alpha_2 z_{2,i,t}, \tag{1}$$

where α and β are regression parameters estimated by the Lahontan MPVA; x and z are covariates (x, stream temperature and peak flow; z, non-native density and riparian vegetation condition). These parameters were combined to estimate an average realized growth rate ($\bar{R}$):

$$\bar{R}_{i,t} = r_{i,t} - \phi_{i,t}\frac{N_{i,t-1}}{E_i}, \tag{2}$$

where E is the spatial extent of stream habitat available to a population and $N_{t\text{-}1}$ is the population size in the previous year. The intrinsic growth rate ($r_{i,t}$) is population growth potential in the absence of intraspecific competition. As population density approaches zero, the expected realized growth rate ($\bar{R}_{i,t}$) approaches the intrinsic growth rate. The effect of density-dependence ($\phi_{i,t}$) is the reduction in realized growth rates expected if population density was increased by 1 fish per km. As population densities approach carrying capacity, realized growth rates decrease to zero.

Stochastic realized growth rates were drawn from a normal distribution, defined by the average realized growth rate ($\bar{R}_{i,t}$) and the MPVA estimate of environmental stochasticity (σ_i), for the population:

$$R_{i,t} \sim \text{normal}\left(\bar{R}_{i,t},\ \sigma_i\right). \tag{3}$$

We prevented realized growth rates $R_{i,t}$ from exceeding intrinsic growth rates $r_{i,t}$ by drawing a new value from the normal distribution in rare instances when this occurred. The population size in the current time step was drawn from a Poisson distribution based on the population size in the previous time step and the realized growth rate:

$$N_{i,t} \sim \text{Poisson}\left(N_{i,t-1}e^{R_{i,t}}\right). \tag{4}$$

This has essentially the same form as the classic Ricker model (Ricker 1954; Wenger et al. 2017; Leasure et al. 2018), but because it is implemented in a stochastic framework constrained by covariates and linked to process and observation models one should not necessarily expect behavior like that of a traditional deterministic Ricker model.

Management Scenarios

In streams where LCT co-occurred with non-native trout, we simulated effects of non-native trout eradication by comparing LCT population forecasts with and without non-natives. Hypothesizing higher environmental stochasticity in streams with non-natives, we first compared estimates of environmental stochasticity between LCT streams with and without non-native trout. Although non-native trout were expected to have strong effects on LCT populations, we assumed the sparsity of non-native trout data would reduce MPVA's ability to capture this effect via this covariate and would, instead, increase environmental stochasticity. Therefore, we considered the need to reduce stochasticity to account for the full effect on LCT of removing non-native trout. A one-way ANOVA verified this need ($p = 0.005$): mean stochasticity among populations without non-natives was 73% of mean stochasticity among populations with non-natives. Accordingly, we reduced stochasticity to 73% of the original value for non-native eradication scenarios by shifting the entire distribution for this parameter and preserving the uncertainty in the effect. Non-native trout densities were forecast at constant values, either 0 (i.e., eradicated) or the most recent observed density in each stream. The random resampling procedure used to forecast other covariates was not used for non-native trout densities because it resulted in unrealistic temporal dynamics of non-native trout densities.

Simulations of LCT reintroductions were applied to currently unoccupied historical streams. We defined the probability of reintroduction success as 1—extinction probability of introduced populations (1—the probability of abundance dropping to 0) over 30 years. For all reintroduction scenarios, we used the global estimate of environmental stochasticity from the Lahontan MPVA model because population-specific estimates were not available for unoccupied streams. We compared success rates of reintroductions under different scenarios. Based on input from managers who have few source populations for LCT reintroductions, our baseline scenario included reintroducing 20 individuals we assumed survived and reproduced at the same rates as resident fish. We also simulated one-time reintroductions of 5, 10, 15, 20, 40, 60, 80, 100, 200, and 1000 fish and different densities (2, 5, 10, 15, 20, and 50 fish/km).

For unoccupied streams with non-native trout, we simulated baseline reintroductions (i.e., 20 LCT) with and without prior non-native eradications. All other reintroduction scenarios were based on the assumption that non-native trout were previously removed. We evaluated the effectiveness of repeated introductions by simulating reintroductions of 20 LCT per year over 3 consecutive years for comparison with one-time reintroductions. We expected repeated reintroductions to intensify the propagule effect (Simberloff 2009; Hufbauer et al. 2013), particularly for streams with poor habitat. Because LCT are managed in distinct geographic management units, assumed to encompass unique geographical, ecological, behavioral, and genetic variation (Fig. 1), we evaluated the success of baseline reintroductions by GMU.

We developed a graphical user interface for the Lahontan MPVA that performed all forecasting procedures (Supporting Information) based on the equations above, parameter estimates from Leasure et al. (2018), and covariates measured annually for each population. This tool was built using the R packages shiny (Chang et al. 2017) and leaflet (Cheng et al. 2017). The interface provides the ability to browse populations on a map and to forecast their dynamics under different management scenarios, including non-native trout eradications, changes in environmental stochasticity, and LCT reintroductions.

Results

Simulations indicated that populations with (30 year) extinction risks approaching zero tended to have >2000 fish (Fig. 2a). Small populations (i.e., <2000 fish and <20 km of stream habitat) with a low chance of extinction always had low estimates of environmental stochasticity. Populations with extinction risks approaching 100% always had high estimates of environmental stochasticity (Fig. 2). These tended to have zeros in one or more years of observation (i.e., no LCT observed during recent surveys) that were not well explained by covariate effects.

Conservation populations tended to have lower extinction risks (mean = 19.8%) than nonconservation populations (mean = 52.7%), but not always (Fig. 3). For example, 2 conservation populations had very high extinction risks. For both, no LCT were captured in the most recent surveys indicating that they may already be extinct. In contrast, the conservation population with the lowest extinction risk had extremely low environmental stochasticity ($\sigma = 0.24$), no non-native trout, and a relatively large spatial extent (17.8 km). Two non-conservation populations also had very low extinction risks. One had low environmental stochasticity ($\sigma = 0.76$), no non-native trout, and LCT observed in every survey year. The other had a low extinction risk despite having a high density of non-native trout (300/km). Lahontan cutthroat trout were observed during all most recent survey years, and this stream was long (28 km) and had low environmental stochasticity that likely contributed to low extinction probability of this population.

Extinction risks were consistently lower in populations with less environmental stochasticity (Fig. 2). Many forecasts changed significantly when we ignored population-specific estimates of environmental stochasticity and instead used the global distribution of this parameter (Fig. 4). For populations with low extinction risks, this tended to increase extinction risks to around 50%. For populations with high extinction risks, use of the global estimate of environmental stochasticity did not strongly affect extinction risks. One population was an exception (Fig. 4); its estimated environmental stochasticity was high ($\sigma = 2.3$), and non-native trout occurred at high densities (about 100/km) before chemical eradications in 2003 and 2010.

Eliminating non-native trout had a strong positive effect on overall carrying capacities for LCT populations, but this alone did not always reduce extinction risks. Eliminating non-natives while simultaneously reducing environmental stochasticity (to the mean for populations without non-native trout or 73% of the mean for populations with non-native trout) substantially reduced extinction risks for most populations, where non-native trout co-occurred with LCT (Fig. 4). Reducing environmental stochasticity addresses an observed effect of non-native trout not captured by the covariate (non-native trout index) alone.

Simulated reintroductions of LCT into historical streams were more likely to succeed if non-native trout were removed first (Fig. 4). Accordingly, we assumed that non-natives were removed in subsequent reintroduction simulations. Once non-native trout were removed, repeated reintroductions over 3 consecutive years increased the probability of success by only up to 4%; the strongest effect was in warm streams. Reintroduction success increased with the number of fish released up to 60 fish, after which releasing more fish provided minimal gains (Fig. 5). Five-to-ten fish/km was a minimal reintroduction number that provided near-maximum reintroduction success (approximately 52% vs. maximum of 53%) (Fig. 5). Cold-water streams of the western GMU had the highest likelihood of successful reintroduction (Supporting Information). However, the very coldest streams did not have the highest reintroduction success (Supporting Information) because these were small headwater streams, where LCT were isolated in very limited spatial extents.

Discussion

As with traditional PVA, we suggest that extinction probabilities produced by MPVA are best interpreted not as absolute but as relative estimates (Ralls et al. 2002) valuable for prioritizing populations and habitats, exploring effects of recovery action alternatives, and addressing uncertainties. Even so, our estimates of extinction probabilities for LCT populations of varying sizes and occupying distinctive habitats across the range were broadly concordant with previously suggested persistence thresholds for inland trout (8–25 km of available stream length and a minimum of 2500 adults [Hilderbrand & Kershner 2000]). We identified exceptions to these

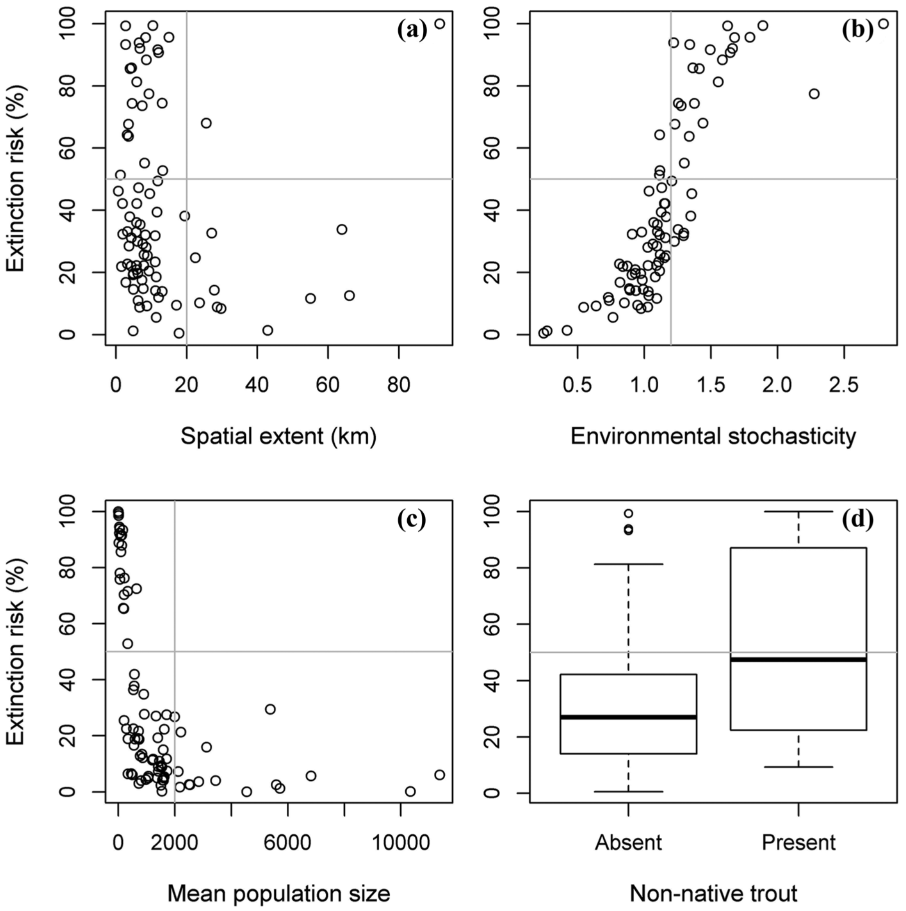

Figure 2. Extinction risk of Lahontan cutthroat trout populations relative to (a) stream extent, (b) environmental stochasticity, (c) abundance, and (d) presence of non-native trout (vertical lines, thresholds beyond which extinction risks tend to be <50%; mid-lines in the boxplots, median values; box ends, interquartile ranges; whiskers, extend to the most extreme data points not exceeding 1.5 times the interquartile range; circles, outliers). Figure modified from Leasure et al. (2018).

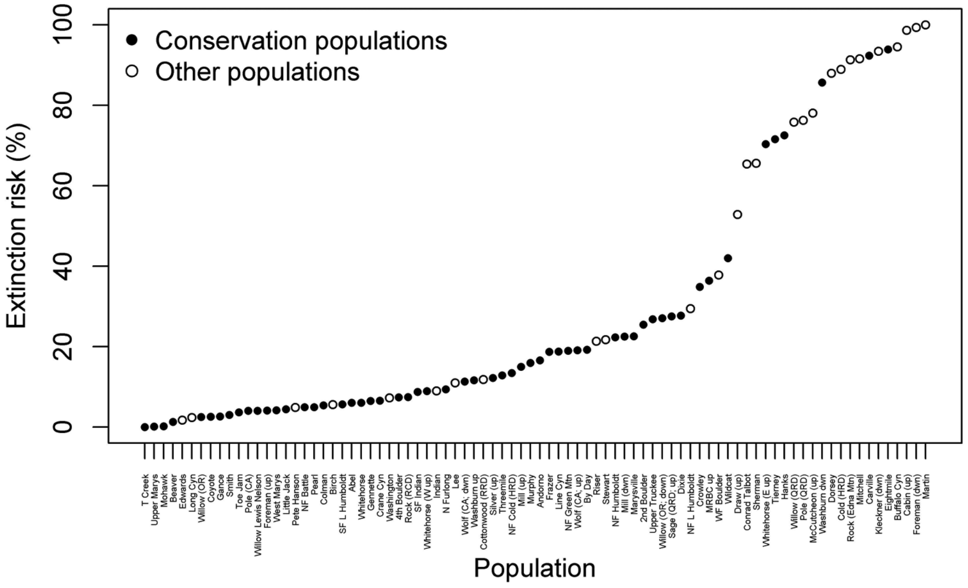

Figure 3. Extinction risks for all Lahontan cutthroat trout populations surveyed.

general rules, either due to variable environmental conditions or stochasticity ignored in simple habitat extent thresholds. Although results confirmed that agency-designated conservation populations—originally identified for their high genetic integrity and assumed resiliency—tended to have lower extinction probabilities relative to other populations, there was notable variation within this category. The MPVA indicated that 6 conservation populations currently assumed to be contributing to range-wide LCT resiliency had a 70% or greater probability of extinction by 2045, and 11 more were at or above 20% risk of extinction. These

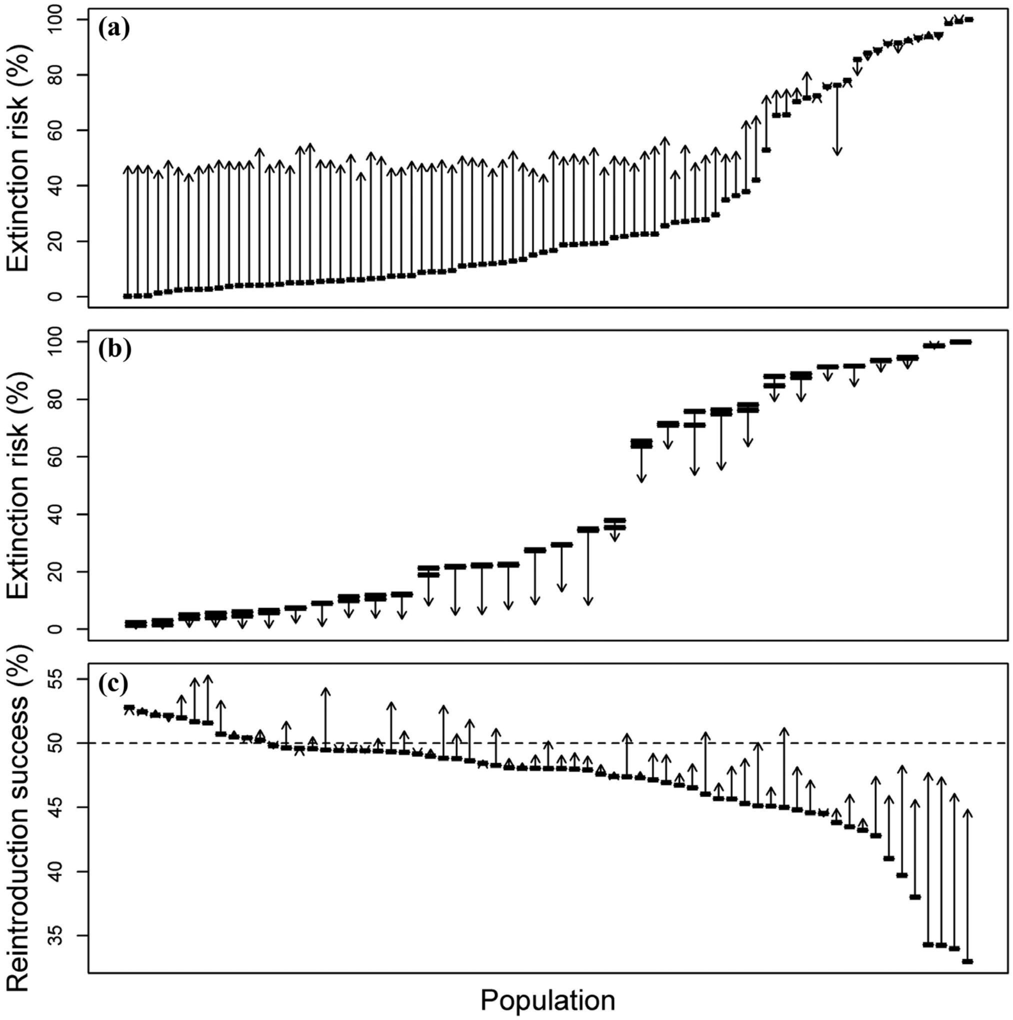

Figure 4. (a) Extinction risk for Lahontan cutthroat trout (LCT) populations estimated using population-specific estimates of environmental stochasticity (arrows, change in extinction risk when the global estimate of environmental stochasticity is used for forecasting), (b) extinction risk for LCT populations in which non-natives occur, based on the most recent observed non-native density for forecasting (small upper horizontal black bar for each population) and change in extinction risk when non-native densities are 0 (small lower horizontal bars for each population) (arrows, change in extinction risk when non-natives are removed and environmental stochasticity is reduced to 73% of its population-specific estimate [difference between group means, see text]), and (c) reintroduction success associated with reintroducing 20 LCT into streams where non-natives occur (arrows, change in reintroduction success when non-natives are removed prior to LCT reintroduction).

populations may be less robust than their conservation designation implies. In contrast, MPVA predicted low (<10%) extinction risk for several non-conservation populations. Collectively, these cases, which would not have been identified otherwise, may merit revised management strategies or designation changes.

Our results confirm the benefit of non-native trout removal for LCT conservation because non-native trout had a strong negative affect on LCT carrying capacities (i.e., a positive effect of the strength of density dependence [Leasure et al. 2018]). Populations with non-native trout also had higher environmental stochasticity, which likely arose in part from poor-quality data for estimating non-native trout densities and trends. Therefore, we suggest reducing environmental stochasticity (here to 73% of stochasticity estimated in the presence of non-natives) when modeling eradications to evaluate the overall effect of removing non-native trout.

The current formulation of MPVA for LCT cannot estimate environmental stochasticity for a population without counts from field surveys. From our comparisons of extinction risk based on population specific versus global estimates, when survey data are not available to help inform estimates of environmental stochasticity (always the case for potential reintroduction sites), extinction risk estimates will always be greater than about 40%.

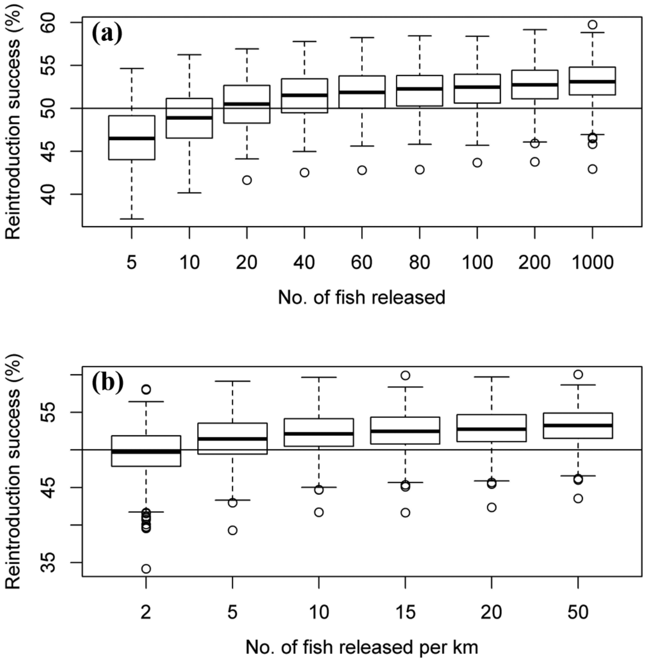

Figure 5. Reintroduction success relative to (a) number of fish released and (b) number of fish released/kilometer (boxes, range; horizontal lines in boxes, mean; whiskers, 1.5 times the interquartile range; circles, outliers).

Because environmental stochasticity is unexplained random variation in estimated population sizes (Supporting Information), it would be ideal to include additional covariates that may explain more of this residual variation (such as sensitivity of streams to drying [Schultz et al. 2017]). A challenge is to develop informative covariates that can be measured every year throughout the entire range of LCT (not the case for stream drying). Another approach would be to develop a variance model that predicts environmental stochasticity based on covariates. This approach would enable population-specific estimates of environmental stochasticity for potential reintroduction sites, where these covariates could be measured and thus improve estimates of persistence.

In addition to assessing the benefit of removing non-native trout, we applied MPVA to estimating reintroduction success. Reintroductions of freshwater fish frequently fail for reasons that may be difficult to explain (Cochran-Biederman et al. 2015). Not evaluating the feasibility of reintroductions in advance of implementing them may contribute to failures (Dunham et al. 2011; Brignon et al. 2017). The MPVA identified several attributes influencing reintroduction success, information that may help in developing management protocols and prioritizing habitats for future reintroductions. For example, MPVA demonstrated that the removal of non-native trout can improve the likelihood of successful reintroductions. This is a common-sense result, but the Lahontan MPVA quantified the effect and identified streams where this was most important; the relative benefit of removing non-native species differed substantially among populations. This finding is consistent with empirical reviews demonstrating that effects of non-native trout on native trout may be highly variable (Dunham et al. 2002). Given that the eradication of non-native trout is costly and success is uncertain (e.g., Meyer et al. 2006; Shepard et al. 2014), an a priori understanding of its relative benefit in waters of interest is useful for management decisions.

Repeating reintroductions provided slight gains in success, particularly in warmer streams. In our MPVA, reintroductions were most successful with either 60 fish or 5–10 fish/km. This reflects LCT's rapid population growth in good-quality habitat (Platts & Nelson 1988). The MPVA generally highlighted higher elevation streams (e.g., in the Sierra Nevada or Ruby Mountains in the western and eastern GMUs, respectively) as the most suitable reintroduction sites for LCT. Lower elevation habitats in the northwest were considerably less likely to sustain reintroduced LCT.

In interpreting the relative estimated success, recall that reintroduction scenarios all used the global distribution of environmental stochasticity (as population-specific estimates were not available for unoccupied habitats), which means that the highest probability of reintroduction success that can be expected is about 60%. However, if there was reason to believe that environmental stochasticity was less than average in a given stream (e.g., based on a nearby sampled population with similar physical and environmental attributes), one would expect increased probabilities of success beyond what we report here. Monitoring reintroductions in the future would provide empirical information useful for adaptive management and verifying model assumptions for further refinement (Parlato & Armstrong 2013; Runge 2013).

Some have argued that PVA should be the primary foundation for delisting threatened and endangered species (Himes Boor 2014). Our application of the Lahontan MPVA provides the framework needed by management agencies to identify and prioritize recovery actions based on empirical data. Still, there are limitations to our approach and broader aspects of recovery to consider (Wolf et al. 2015). First, we relied on found data that may not be representative of LCT populations and habitats. Conservation populations are sampled more often than others, and the best habitats within a population's extent are often targeted for sampling. Moving toward a more randomized but spatially and temporally balanced sampling design may reduce bias and improve inferences range-wide. Additionally, as is common with PVA (Allendorf & Ryman 2002), ours is a demographic model that does not include genetic effects on population viability. Extinction can have both short- and long-term genetic drivers (Newman & Pilson 1997; Saccheri et al. 1998; Frankham 2005), which are likely most important for the small and isolated populations typically evaluated with PVA (Allendorf & Ryman 2002). Observations of low effective sizes and severe bottlenecks suggest genetic risks in some LCT populations (Neville et al. 2006; Peacock & Dochtermann 2012), for which the Lahontan MPVA may underestimate the true extinction risk. Accordingly, it may be important to consider not only needs for near-term persistence, but also ways to maintain evolutionary processes promoting long-term viability (Moritz 2002). Other components of resiliency, such as life-history variability (Dunham & Rieman 1999; Kendall et al. 2014) or unique ecological or evolutionary traits (Gustafson et al. 2007; Hutchings et al. 2012), could be included in a conservation portfolio (Schindler et al. 2010; Haak & Williams 2012; Schindler et al. 2015). A 3 R's approach could be used to ensure population representation, resiliency, and redundancy (Wolf et al. 2015). Finally, our forecasts were based on the assumption that future and historical conditions will be similar. Further simulations would be required to evaluate the effects of climate change and other mechanisms that could cause significant deviations from historical conditions in the future.

An MPVA provides a quantitative tool that can link recovery criteria and management actions to empirically demonstrated reductions in extinction risk (Doak et al. 2015), and our application highlights new capabilities relative to past spatial prioritization methods applied to native trout conservation (e.g., Peterson et al. 2013; Falke et al. 2014; Roy & Le Pichon 2017). Beyond trout, this novel framework extends the reach of quantitative PVA to any at-risk species with multiple isolated populations, where it is difficult to collect data for traditional PVA (example species in this geography include American pika [*Ochotona princeps*], greater sage grouse [*Centrocercus urophasianus*], and pygmy rabbit [*Brachylagus idahoensis*]). Finally, in the United States and elsewhere, there is an increasing emphasis on prelisting and proactive conservation (e.g., Cardillo et al. 2006; Scott 2006; Baruch-Mordo et al. 2013). The MPVA framework can support the identification and prioritization of cumulatively effective proactive conservation actions that could reduce the potential for future listing needs (e.g., Drechsle et al. 2011).

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Supporting Information

A detailed description of environmental stochasticity and its importance in model interpretation and a graph of estimated reintroduction success by geographic management unit and stream temperature (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. An interactive user interface (R Shiny application) to simulate population dynamics of Lahontan cutthroat trout under different management scenarios to estimate extinction risk and reintroduction success is available on Figshare (https://doi.org/10.6084/m9.figshare.9121958.v1).

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