

RESEARCH ARTICLE

Assessment across life stages reveals superior habitat suitability in reintroduced historical habitats for an endangered salmon species

Shih-Fan Chan¹  | Mark Liu¹ | Dustin R. Rubenstein^{2,3}  | Yi-An Chung^{1,4} | Wei-Ren Lin^{1,5} | Lin-Yan Liao⁶ | Sheng-Feng Shen^{1,4,5} 

¹Biodiversity Research Center, Academia Sinica, Taipei, Taiwan; ²Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA; ³Center for Integrative Animal Behavior, Columbia University, New York, New York, USA; ⁴International Degree Program in Climate Change and Sustainable Development, College of Science, National Taiwan University, Taipei, Taiwan; ⁵Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan and ⁶Wuling Station, Shei-Pa National Park, Taichung, Taiwan

Correspondence

Sheng-Feng Shen

Email: shensf@sinica.edu.tw**Funding information**

Shei-Pa National Park, Taiwan, Grant/

Award Number: SP111121

Handling Editor: Aashna Sharma**Abstract**

1. Accurate assessment of habitat suitability is crucial for the conservation of endangered species. However, conventional measures often overlook the complexity of ecological requirements across life stages and how different causes of local extinctions (e.g. habitat degradation versus overharvesting) can lead to misinterpretation of optimal habitat conditions. We investigated how life-stage specific ecological requirements and historical causes of population decline affect habitat suitability assessment in the critically endangered Formosan landlocked salmon (*Oncorhynchus masou formosanus*).
2. We compared Chichiawan Creek (a remnant population) with Hehuan Creek (a reintroduced population) using field surveys and in situ experiments. We quantified redd density, nest site selection and hatching rates. We also estimated multidimensional niche hypervolumes based on five key aquatic environmental parameters (water temperature, conductivity, pH, dissolved oxygen and stream velocity) for the nesting and hatching stages, and assessed the influence of these factors on reproduction and early development.
3. Habitat suitability, defined as the relationship between environmental variables and species' fitness, was higher in Hehuan Creek than Chichiawan Creek for both the nesting and hatching stages. The hatching hypervolume was substantially smaller (49.5%) than the nesting hypervolume, indicating more stringent environmental requirements for successful egg development compared to adult nesting behaviour, and representing a critical ecological bottleneck for conservation planning.
4. Redd density increased with stream velocity but decreased with water conductivity and temperature. Female salmon selected nest sites with lower stream velocities,

Shih-Fan Chan and Mark Liu contributed equally to this work.

© 2025 The Author(s). Journal of Applied Ecology © 2025 British Ecological Society.

more neutral pH values, lower conductivity and higher dissolved oxygen levels. Hatching success was most strongly associated with lower water conductivity, temperature and moderate stream velocity, while indicators of eutrophication levels (dissolved oxygen and pH) had less influence on egg development.

5. *Synthesis and applications.* Our results challenge the assumption that remnant habitats represent optimal conditions for endangered species, especially when historical local extinctions were caused by overharvesting rather than habitat degradation. This study provides a framework for comprehensive conservation strategies that integrate historical distribution data with quantitative assessments of stage-specific ecological requirements for salmonids. This approach will enable conservation practitioners to better identify suitable areas for protection and reintroduction, improving endangered species management under rapid environmental change.

KEYWORDS

endangered species conservation, Formosan landlocked salmon, habitat suitability, life stage, niche space, *Oncorhynchus masou formosanus*, reintroduction

1 | INTRODUCTION

In the context of rapidly declining global biodiversity, in situ conservation and species reintroduction have become key strategies for protecting endangered species (IUCN/SSC, 2013; Seddon et al., 2014). However, these methods face new challenges from global environmental change and therefore require constant adaptation. Understanding the historical factors driving species decline is crucial for effective conservation (Armstrong & Seddon, 2008). When habitat degradation drives extinctions, remnant populations often persist in remaining high-quality habitats (Brown, 1995; Johnson, 2004; Lawton et al., 1995; Pulliam, 1988; Pulliam & Danielson, 1991). In such cases, the distribution of remnant populations may better reflect the environmental needs of the species, providing a reliable guide to conservation strategies. Although conservation practitioners often assume that remnant populations occupy optimal habitats, this assumption may not hold true if factors other than habitat degradation are the primary cause of decline (IUCN/SSC, 2013). When population declines stem from human exploitation (e.g. overharvesting) (Yackulic et al., 2011) or sudden natural disasters (Walters, 1997), the situation becomes more complicated for habitat assessment and conservation planning. Unlike habitat degradation that preserves the habitat–population relationship, these non-habitat factors can eliminate populations from optimal habitats while leaving populations in marginal areas that happen to escape exploitation or disaster impacts. These same factors can affect even optimal habitats, leading to remnant populations occurring in suboptimal areas (Channell & Lomolino, 2000). Thus, assessing habitat suitability based only on current population distributions can be misleading. Holistic conservation strategies require the integration of habitat restoration, reduction of anthropogenic pressures

(including overfishing) and targeted interventions that minimize human-induced ecosystem disturbances, such as pollution, altered hydrological regimes and recreational impacts. These evidence-based approaches, combined with carefully planned reintroductions guided by comprehensive scientific assessments, provide the foundation for effective species recovery.

Accurately assessing habitat suitability requires evaluating species' biotic and abiotic requirements across different life stages as well as quantifying species–environment interactions using robust empirical approaches (Armstrong et al., 2003; IUCN/SSC, 2013). Moreover, assessing habitat suitability using short-term establishment of reintroduced populations can misrepresent long-term species viability and population dynamics, since the factors driving initial establishment are often different from those required for long-term persistence (Armstrong & Seddon, 2008; Iles et al., 2016; Robert et al., 2015). Species may thrive initially but later face challenges like resource depletion or increased competition (Iles et al., 2016; Robert et al., 2015). In conservation practice, reintroduction sites are often chosen based on two simple but potentially misleading criteria: (i) the focal species previously existed at the site; or (ii) the site meets basic habitat criteria for the species based on current observable conditions (Osborne & Seddon, 2012). However, this approach may overlook key ecological processes and long-term adaptive mechanisms. Failure to adequately address the initial causes of species decline and recognize unsuitable habitat conditions (e.g. water quality and availability of food or reproductive resources) has been shown to be the most important predictors of reintroduction failure (Cochran-Biederman et al., 2015; Godefroid et al., 2011). These findings highlight the limitations of relying solely on historical records or simple habitat characteristics when planning reintroductions. Instead, reintroduction sites should be selected using a systematic

approach to comprehensively assess habitat suitability, including addressing initial causes of decline, accurately quantifying existing habitat conditions and simulating the effects of future environmental changes (Cochran-Biederman et al., 2015; Osborne & Seddon, 2012).

Recent work has increasingly shown that considering the environmental requirements of only a single life stage can lead to serious misjudgements of habitat suitability. For example, research on Atlantic salmon, brown trout and Arctic charr has emphasized that eggs and juveniles have more stringent requirements than adults for water quality, flow and substrate characteristics (Armstrong et al., 2003; Elliott & Elliott, 2010). For these salmonid species, eggs consistently have the lowest temperature tolerance of all life stages, making them particularly vulnerable to climate change. Building on these earlier findings, a comprehensive meta-analysis examining 694 marine and freshwater fish species from all climate zones, including 34 species or subspecies of salmonids, demonstrated that spawning adults and embryonic stages have the narrowest thermal tolerance ranges, making them less tolerant to warming water than juveniles and non-breeding adults (Dahlke et al., 2020). This finding further confirms the inherent limitations of approaches that consider only a single life stage for conservation management. As a result, some habitats may be suitable for adults but not for reproduction or juvenile development, potentially leading to long-term population declines. These studies highlight that focusing solely on adult requirements overlooks critical developmental stages necessary for population persistence. Therefore, a comprehensive assessment of habitat suitability must consider the diverse needs of a species throughout its life cycle.

Here, we use the Formosan landlocked salmon (*Oncorhynchus masou formosanus*), an endangered subspecies endemic to Taiwan, to develop an integrated approach for comprehensive habitat suitability assessment. The Formosan landlocked salmon is found exclusively in the upper reaches of the Dajia River in Taiwan (Figure 1a), representing the southernmost natural salmon population in the Western Pacific (Morita, 2018; Oshima, 1936). Since the 1950s, this population has experienced a severe population decline (Lin et al., 2004; Zheng, 1987), with a population bottleneck of approximately 200 individuals remaining in a 5 km stretch of Chichiawan Creek in 1984 (Lin & Chang, 1989). Since the late 1980s, several in situ restocking programs and habitat restoration efforts have been undertaken in Chichiawan Creek. In addition, since 2017, a reintroduction program was initiated in Hehuan Creek, a historical habitat where the species once existed but later became extinct. According to a long-term study documenting the historical population trends of Formosan landlocked salmon since 1950, the construction of the Central Cross-Island Highway in central Taiwan in 1956 allowed gold miners to enter Hehuan Creek. This access led to extensive overfishing (using ichthyotoxins and electrofishing) between 1956 and 1969, ultimately resulting in the local extinction of the Hehuan Creek salmon population (Zheng, 1987). This finding strongly suggests that the primary cause of the historical local extinction of Formosan landlocked salmon may have been due to anthropogenic factors rather than

habitat degradation. Consequently, Hehuan Creek may not necessarily be inferior to Chichiawan Creek as a habitat for Formosan landlocked salmon, and the reintroduction efforts there provided an opportunity to assess its suitability for the recovery of the species.

Our study has three key objectives: (1) to determine whether habitat suitability differs between remnant and historical habitats, challenging the common assumption that remnant populations persist in optimal conditions; (2) to quantify how environmental requirements vary across different life stages (particularly nesting and hatching), testing the hypothesis that reproductive stages have more stringent environmental requirements than adult survival; and (3) to identify critical environmental factors that influence population persistence at each life stage. We predict that if historical local extinctions were primarily driven by anthropogenic factors like overharvesting rather than habitat degradation, Hehuan Creek may provide equivalent or superior habitat conditions compared to Chichiawan Creek. Our approach integrates comparative field surveys of population dynamics, redd distribution and hatching success with experimental assessments of stage-specific habitat requirements. By quantifying niche hypervolumes based on five key aquatic environmental parameters (water temperature, conductivity, pH, dissolved oxygen and stream velocity) for different life stages and analysing the contribution of each creek to these niche spaces, we provide a comprehensive framework for habitat suitability assessment that accounts for both historical distribution patterns and life-stage-specific requirements. This integrated approach has broad implications for conservation strategies, particularly for endangered species whose current distributions may not reflect their complete ecological requirements.

2 | MATERIALS AND METHODS

2.1 | Study area

In 2021 and 2022, we conducted the study in two creek systems in the upper reaches of the Dajia River (Figure 1a) in Taiwan. Chichiawan Creek (Figure 1b) is the last known natural habitat of the remnant population of Formosan landlocked salmon. Hehuan Creek (Figure 1c) is a historical habitat in which the salmon went extinct by the late 1960s and was the focus of a comprehensive reintroduction program between 2017 and 2019 (Figure 1d). This reintroduction program established three sectors within Hehuan Creek: Taiyang City, Huagang Tribe and Hehuan Creek Trail. Initial reintroduction efforts began in October 2017 with the release of 900 juvenile salmon (age 0+), followed by subsequent releases of 3000 juveniles in 2018 and 2400 juveniles in 2019, all within their first year of life (0+) (Liao et al., 2024). Our study was conducted beginning in 2021, 4 years after the first reintroduction in 2017, allowing sufficient time for multiple generations of the reintroduced population to establish. We selected eight sectors within these creeks: Dam 4 (ca. 1900m in elevation), Dam 3 (ca. 1830m), Dam 2 (ca. 1780m), Dam 1 (ca. 1760m), Taiwan Salmon Eco Center (ca. 1720m), Wuling Guest House (ca. 1690m) in Chichiawan Creek and Hehuan Creek

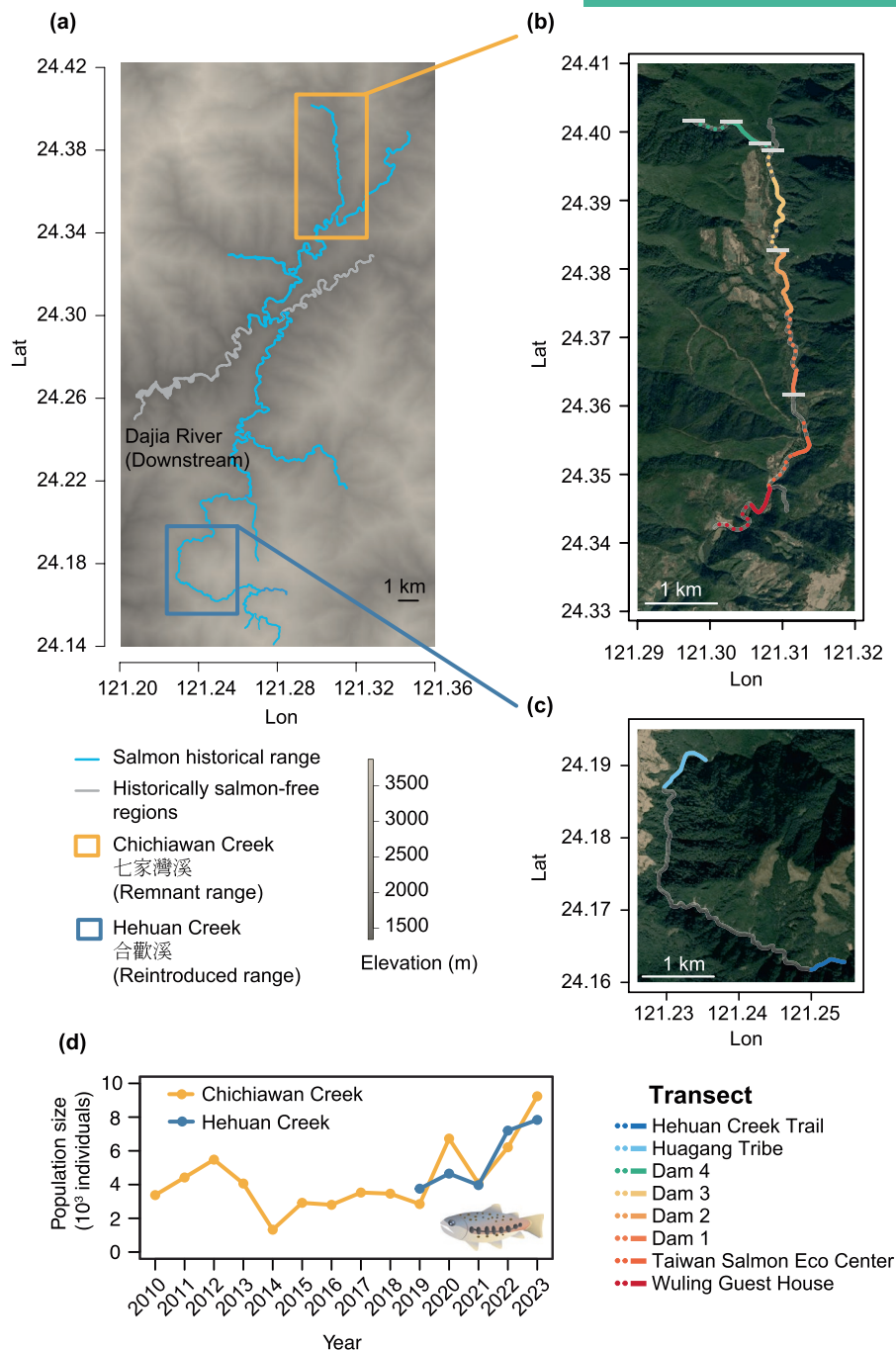


FIGURE 1 Study sites. (a) Historical range of the Formosan landlocked salmon and the locations of our study sites. (b, c) A real map for (b) Chichiawan Creek and (c) Hehuan Creek. (d) Salmon population trends in the two study creek systems. In (b) and (c), transparent white lines represent the creeks. Lines with different colours represent different sites, with solid lines indicating transects where redd density was surveyed, and dashed lines marking areas for population density survey and hatching experiment.

Trail (ca. 2550m) and Huangang Tribe (ca. 2250m) in Hehuan Creek (Figure 1b,c).

2.2 | Field survey and experiment

We obtained salmon density data for 2021 and 2022 from annual snorkelling surveys conducted by volunteers in both creeks in

Shei-Pa National Park (see [Supporting Information](#)). These surveys have been conducted annually since 1987 (Chung et al., 2007). We also surveyed for salmon redds, or rows of nests constructed by a single female salmon that are formed when she uses her tail and flanks to excavate and cover one or more depressions in the gravel to protect fertilized eggs during incubation (Fleming et al., 1996). We identified redds by observing salmon nesting behaviour in combination with distinct site characteristics, such as newly disturbed gravel,

visible depressions or fresh gravel mounds, which typically indicate an active redd. We established a transect at each study sector to survey for salmon redds and visited each transect every 5–6 days throughout the 2021 and 2022 breeding seasons to locate and record any new redds. We also randomly selected sites for further environmental comparison with redd sites. We divided the study reaches of Chichiawan Creek and Hehuan Creek into 1364 and 1119 cells on the aerial map, respectively, and randomly selected cell numbers to determine these random sites.

We also conducted in situ hatching experiments to investigate how environmental variables affect the hatching rate of salmon eggs. For these experiments, we specifically selected only natural redd sites identified in our previous surveys ($n=17$ in Chichiawan Creek; $n=15$ in Hehuan Creek) that represented different environmental conditions. We installed three replicate Whitlock-Vibert boxes (Whitlock, 1977) at each of these natural redd sites to deposit salmon eggs obtained from a single captive population. By using only natural redd locations, we aimed to understand how the environmental conditions at sites naturally selected by salmon for spawning affect hatching success. This semi-manipulative field experimental design controlled for egg quality and deposition conditions while utilizing natural environmental gradients across sites. We standardized egg sources, placement depth and substrate conditions, allowing us to isolate the effects of aquatic environmental variables on hatching success. After 3 weeks, we retrieved the boxes and counted the number of successfully hatched alevins, enabling systematic comparison of hatching rates across varying environmental conditions. For each redd site, random site and experimental site (with Whitlock-Vibert boxes), we measured pH, dissolved oxygen, conductivity, stream velocity and water temperature for further analysis. Detailed information on survey methods, experimental procedures and measurement techniques is provided in the Supporting Information (Appendix S1).

Permits for the field study were issued by Shei-Pa National Park (1110002834) for Chichiawan Creek and by Taroko National Park (1110003283) for Hehuan Creek. Permits for the experimental use of salmon eggs were issued by the Forestry Bureau of Taiwan (1101611340, 1111701591). This study did not require additional ethical approval according to the regulations in Taiwan.

2.3 | Data analysis

We used linear mixed models (LMMs; *lme4* package; Bates et al., 2015) to assess environmental effects on redd density among transects, with transect ID as a random factor. To analyse nest site selection and hatching success at microhabitat (site) level, we employed two complementary approaches: (1) generalized linear mixed models (GLMMs) for interpretable individual variable effects; and (2) Random Forest with SHapley Additive exPlanations (SHAP) to handle complex non-linear relationships and provide objective assessments of effect sizes.

For nest site selection, we used a binomial GLMM with a binary response (1 = redd site, 0 = random site) with transect ID as a random

factor. For hatching success, we used a negative binomial GLM (MASS package; Venables & Ripley, 2002) to compare differences among transects, and a negative binomial GLMM with hatched alevins as the response variable, $\log(\text{total egg number})$ as an offset term and transect ID as a random factor. We used the *randomForest* package (Liaw & Wiener, 2002) and the *shapviz* package (Mayer & Stando, 2023) for Random Forest and SHAP analyses, respectively.

To address multicollinearity, we also performed principal component analysis (PCA) on aquatic environmental variables (pH, stream velocity, dissolved oxygen, conductivity, water temperature) and used the resulting components as predictors in separate models.

To quantify differences in ecological niches between nesting and hatching stages, we estimated hypervolumes using the Gaussian kernel density approach (Blonder et al., 2014, 2018). After performing PCA on the pooled environmental data, we constructed separate hypervolumes for nesting and hatching in PCA space. We used permutation MANOVA (*adonis2* function in *vegan* package; Oksanen et al., 2022) to test for differences between these hypervolumes. We calculated the overlap between nesting and hatching hypervolumes and estimated the unique contribution of each creek and transect to both hypervolumes using the *hypervolume_set* function (Blonder et al., 2014, 2018).

For spatial visualization of habitat suitability, we projected predicted nesting and hatching probabilities onto creek maps using loess regression (*stats* package; R Core Team, 2022). We calculated overall habitat suitability as the square root of the product of nesting and hatching probabilities. All analyses were performed using R v4.2.1 (R Core Team, 2022), with detailed methods provided in the Supporting Information (Appendix S1).

3 | RESULTS

3.1 | Niche hypervolume analysis of nesting and hatching stages

Our hypervolume analysis quantified the environmental niche spaces during the nesting ($n=283$ redd sites and 205 random points) and egg hatching ($n=190$ from 32 sites) stages of the Formosan landlocked salmon. PCA of the environmental variables revealed three major independent environmental dimensions (Figure 2; Figure S1; Table S1). PC1 explained 40.2% of the variation, representing temperature-related stress, and was positively related to mean water temperature and conductivity (Figure 2; Table S1). PC2 explained 26.2% of the variation and was associated with eutrophication, positively correlated with daytime pH and negatively correlated with dissolved oxygen and stream velocity (Figure 2; Table S1). PC3 explained 14.9% of the variation and was primarily positively correlated with stream velocity (Figure S1; Table S1).

The permutation MANOVA revealed that nesting and hatching hypervolumes differed significantly in their position across these environmental dimensions ($F=35.20$, $p=0.001$; Figure 2). The hypervolume overlap analysis showed only 25.9% overlap between

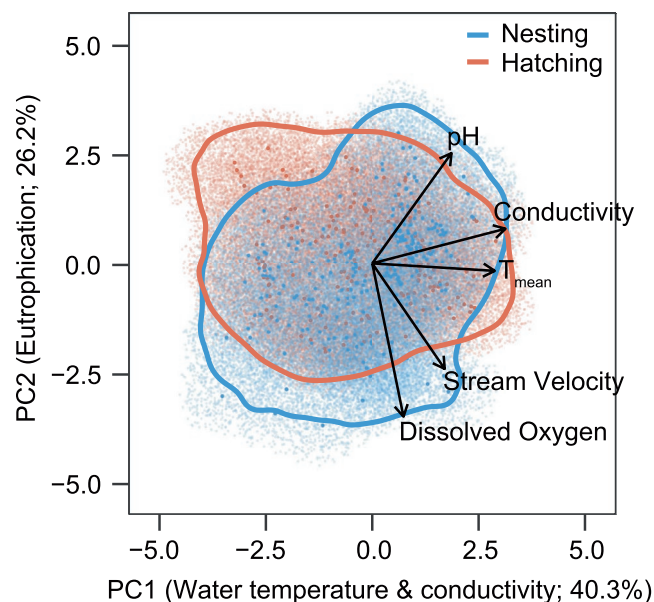


FIGURE 2 Nesting and hatching hypervolumes of the Formosan landlocked salmon. The data points and estimated hypervolumes are projected on the environmental PCA biplot with the first two principal components (PC1 and PC2). The solid points indicate actual field samples (blue for nesting sites and orange for hatching sites with observed hatching rates above zero). The semi-transparent points were generated through resampling with the R function *kernel.build*. The encircled regions are kernel density estimations for the hypervolumes. Arrows show the direction and strength of the correlation between environmental variables and principal components. T_{mean} denotes mean water temperature.

the two stages, indicating distinct environmental requirements for nesting versus hatching. Additionally, the hatching hypervolume was 49.5% (313.6/634.1) the size of the nesting hypervolume, suggesting more stringent environmental conditions for successful hatching compared to initial nest site selection.

3.2 | Effects of environmental variables on salmon redd density at the transect level

The field survey revealed substantial variation in redd density across transects, with the highest densities observed at Huagang Tribe and Hehuan Creek Trail (approximately 0.018 and 0.014 redds/m², respectively) and the lowest density at the Taiwan Salmon Eco Center (approximately 0.001 redds/m²) (Figure 3a).

Our linear mixed models analysing environmental effects on redd density showed that redd density decreased significantly with increasing conductivity (LMM, $p=0.01$; Figure 3b; Table S2a), which was highly correlated with water temperature ($r=0.87$). When we excluded conductivity from the model, temperature showed a negative effect on redd density approaching statistical significance ($p=0.057$; Figure 3c; Table S2b), though model performance decreased when excluding conductivity (R^2_m decreased from 0.57 to 0.46). Neither dissolved oxygen (LMM, $p=0.17$; Figure 3d) nor pH

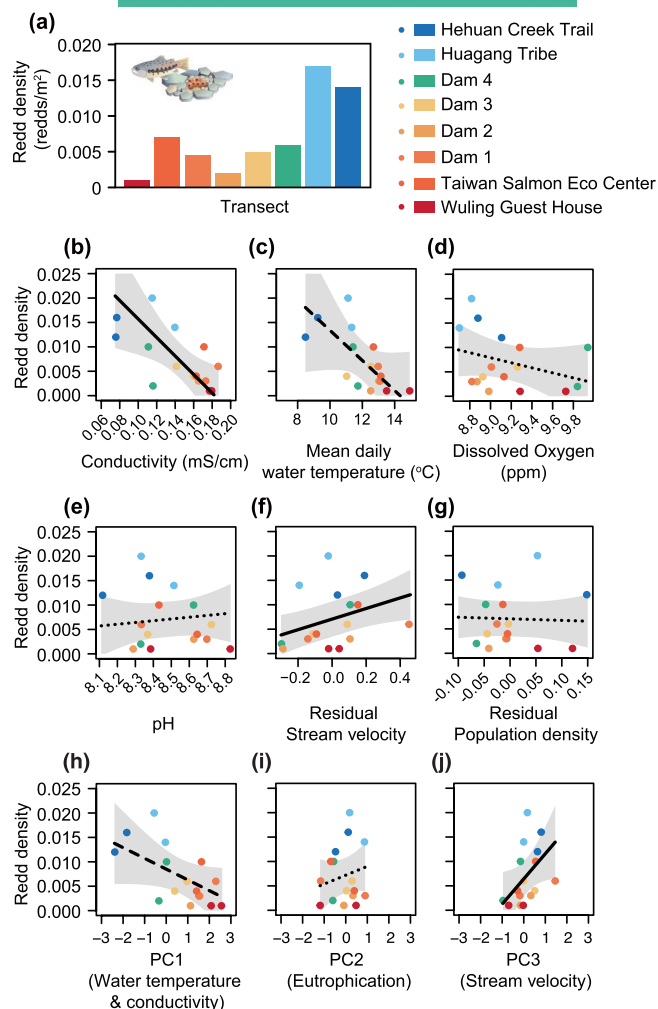


FIGURE 3 Environmental factors affecting salmon redd densities. (a) Redd densities among sites. (b–g) Effect of environmental variables and population density on redd density. (h–j) Effect of environmental principal components on redd density. In panel (a), the bars represent the mean redd densities of the two survey years. In panels (b)–(j), points represent samples, while trends and confidence intervals are estimated using negative binomial GLMMs. Solid lines represent significant trends ($p \leq 0.05$), dashed lines represent marginally significant trends ($0.05 < p \leq 0.10$), and dotted lines represent non-significant relationships ($p > 0.10$).

(LMM, $p=0.57$; Figure 3e; Table S2a) had significant effects on redd density. After controlling for other factors, stream velocity showed a significant positive correlation with redd density (LMM, $p=0.03$; Figure 3f; Table S2a), while population density had no significant effect (LMM, $p=0.80$; Figure 3g; Table S2a).

When using principal components as predictors in our models, we found that high PC1 (representing water temperature and conductivity) also reduced redd density approaching statistical significance (LMM, $p=0.06$; Figure 3h; Table S2c), and high PC3 (representing high flow velocity) promoted a significant increase in redd density (LMM, $p=0.03$; Figure 3i; Table S2c), whereas PC2 (eutrophication) showed no apparent effect (LMM, $p=0.29$; Figure 3j; Table S2c). These results collectively demonstrate that at the transect level,

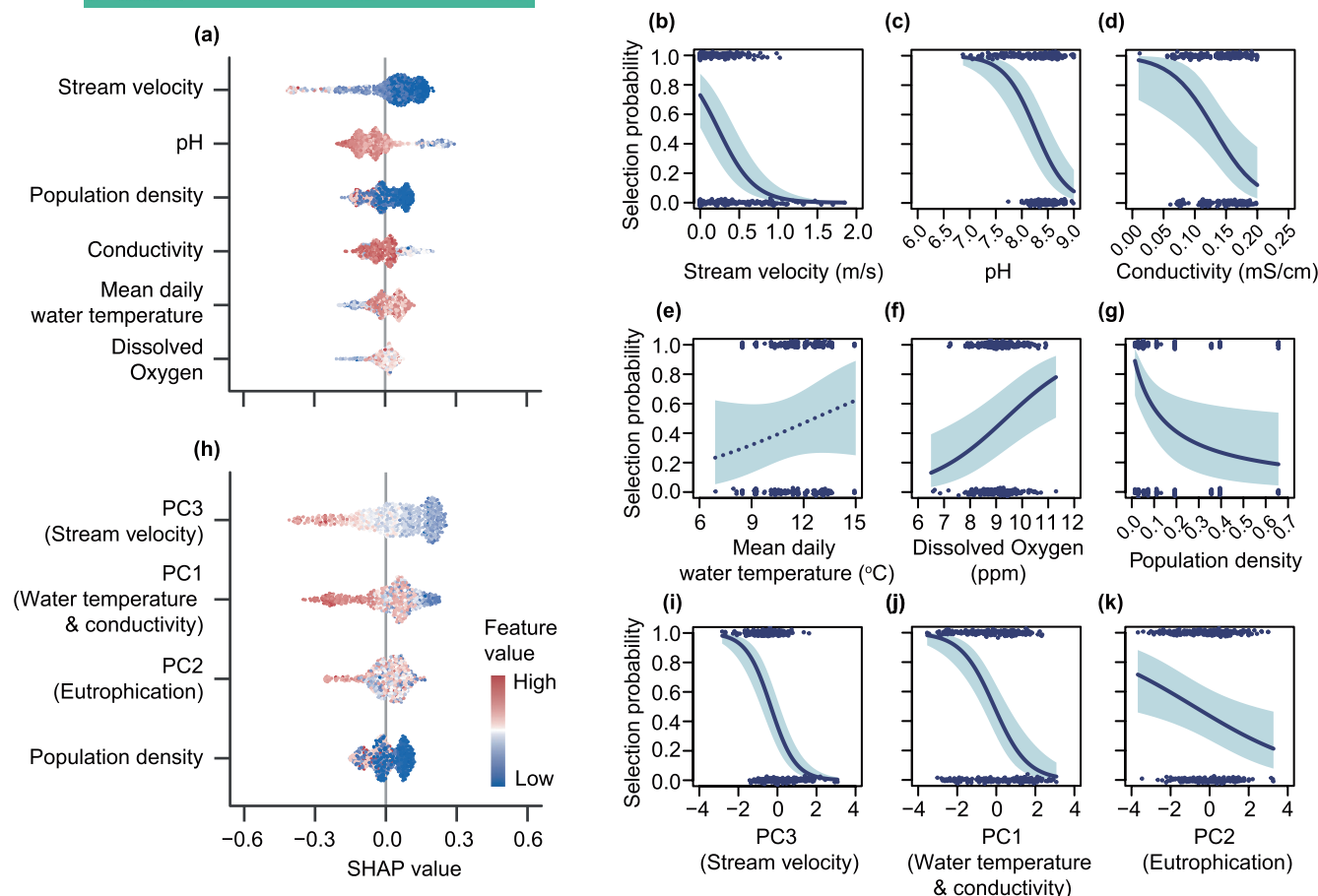


FIGURE 4 Environmental factors affecting salmon nest site selection. (a) SHAP (SHapley Additive exPlanations) summary plot for the effect sizes of environmental variables and population density on salmon nest site selection. (b–g) Effects of environmental variables and population density. (h) SHAP summary plot for the effect sizes of environmental principal components. (i–k) Effect of environmental principal components. In panels (a) and (h), the vertical axis lists features (environmental variables or principal components) ranked by importance, with the most critical features at the top. The horizontal axis displays the SHAP values, indicating the extent to which each feature affects the model's output. Point colours represent feature values, with each point corresponding to an individual sample and illustrating how the feature value affects the prediction for that sample. The two SHAP summary plots illustrate the effect sizes of environmental variables and population density, while the effect sizes of sites are shown in Figure S2. In panels (b)–(g) and (i)–(k), points represent samples, whereas trends and confidence intervals are estimated using binomial GLMMs. Solid lines represent significant trends ($p \leq 0.05$) and dotted lines represent non-significant relationships ($p > 0.05$). Points are jittered along the vertical axes for clarity, and points closer to one indicate nesting sites, whereas points closer to zero indicate random sites.

cooler, less ion-rich and faster-flowing streams tend to have higher redd densities.

3.3 | Effects of environmental variables on salmon nest site selection at the microhabitat level

At the microhabitat level, we examined the relative contributions of environmental variables to salmon nest site selection based on estimated effect sizes (mean absolute SHAP values; Figure 4a). Our GLMM analysis revealed that salmon nest site selection was associated with lower stream velocities ($p < 0.001$; Figure 4b; Table S3a), pH values closer to neutral ($p < 0.001$; Figure 4c; Table S3a) and lower conductivity ($p = 0.003$; Figure 4d; Table S3a). Notably, water temperature had an effect size close to conductivity in the SHAP analysis (Figure 4a), but showed a non-significant relationship with

nest site selection in the GLMM ($p = 0.23$; Figure 4e; Table S3a), likely due to its high correlation with conductivity. Salmon also favoured waters with higher dissolved oxygen (GLMM, $p = 0.002$; Figure 4f; Table S2a). In addition to these aquatic environmental parameters, salmon density negatively influenced nesting probability (GLMM, $p = 0.008$; Figure 4g; Table S3a). The SHAP effect size of population density ranked after stream velocity and pH and was larger than all other environmental variables (Figure 4a).

Our supplementary analysis using principal components provided additional insights. In the GLMM analysis, stream velocity (PC3) emerged as the most influential factor on nest site selection ($p < 0.001$; Figure 4h,i; Table S3b), followed by water temperature and conductivity (PC1) ($p < 0.001$; Figure 4h,j; Table S3b), and finally eutrophication level (PC2) ($p = 0.01$; Figure 4h,k; Table S3b). The smaller effect size of salmon density compared to all environmental principal components in the SHAP analysis (Figure 4h) suggests

that correlations between variables may have underestimated the importance of environmental features in the previous model, and that the principal components better capture their importance.

3.4 | Effects of environmental variables on hatching rate

Our hatching experiment showed substantial variation in hatching success across transects. Huagang Tribe and Hehuan Creek Trail in

Hehuan Creek had the highest hatching rates, followed by Dam 4 in Chichiawan Creek, while Wuling Guest House in Chichiawan Creek had the lowest hatching rate (Figure 5a).

We examined the relative contributions of environmental variables to salmon egg hatching rates based on estimated effect sizes (mean absolute SHAP values; Figure 5b). Our GLMM analysis revealed that higher hatching rates were associated with sites having lower stream velocities ($p=0.003$; Figure 5c; Table S4a), pH values closer to neutral ($p=0.02$; Figure 5d; Table S4a) and conductivity around 0.117 mS/cm (conductivity, $p=0.12$; conductivity²,

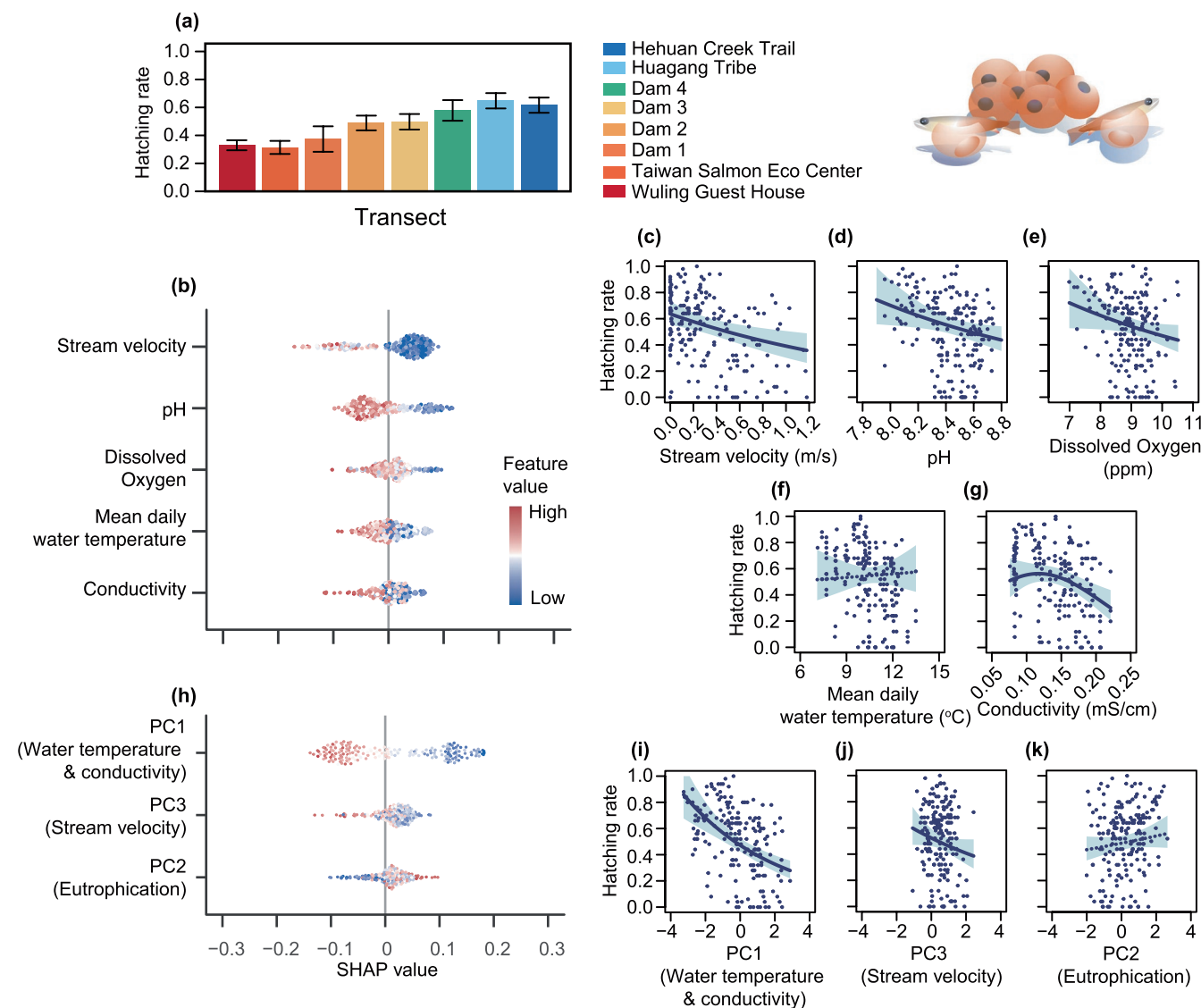


FIGURE 5 Environmental factors affecting salmon egg hatching rate. (a) Hatching rates among sites (b) SHAP (SHapley Additive exPlanations) summary plot for the effect sizes of environmental variables on hatching rate. (c–g) Effects of environmental variables. (h) SHAP summary plot for the effect sizes of environmental principal components. (i–k) Effects of environmental principal components. In panel (a), bars indicate mean hatching rate and error bars indicate standard errors estimated from GLM. In panels (b) and (h), the vertical axis lists features (environmental variables or principal components) ranked by importance, with the most critical features at the top. The horizontal axis displays the SHAP values, indicating the extent to which each feature affects the model's output. Point colours represent feature values, with each point corresponding to an individual sample and illustrating how the feature value affects the prediction for that sample. The two SHAP summary plots illustrate the effect sizes of environmental variables, whereas the effect sizes of sites are shown in Figure S3. In panels (c)–(g) and (i)–(k), points represent samples, while trends and confidence intervals are estimated using negative-binomial GLMMs. Solid lines represent significant trends ($p \leq 0.05$), and dotted lines represent non-significant relationships ($p > 0.05$).

$p=0.04$; Figure 5e; Table S4a). Water temperature did not significantly affect hatching rates in the GLMM ($p=0.74$; Figure 5f; Table S4a). Sites with higher dissolved oxygen showed significantly lower hatching rates (GLMM, $p=0.05$; Figure 5g; Table S4a).

It is worth noting that in the SHAP analysis, conductivity and water temperature had the smallest effect sizes, while dissolved oxygen had only a slightly larger effect (Figure 5b), which is inconsistent with the results of significance tests and could be due to the high correlation between the explanatory variables. To address these potential model uncertainties, we conducted further analysis using principal components. The GLMM results showed that water temperature and conductivity (PC1) had the greatest impact on hatching ($p<0.001$; Figure 5h,i; Table S4b), followed by stream velocity (PC3) ($p=0.05$; Figure 5h,j; Table S4b), while eutrophication (PC2; correlated with dissolved oxygen levels) had no significant effect on hatching rates ($p=0.20$; Figure 5h,k; Table S4b). These results suggest a greater indirect influence of water temperature on hatching rate through water conductivity (potentially determined by dissolved ionic concentration) than on nest site selection.

3.5 | Differential contributions of creeks to salmon niche space

We visualized the nesting probability (redd density $\times$ nest site selection probability) and hatching rates estimated by our GLMMs and Random Forest models on a two-dimensional plane constructed by PC axes (Figure 6a,b). Further analysis of the contributions of Chichiawan Creek and Hehuan Creek to the nesting and hatching hypervolumes revealed that these two creeks contributed to different portions within both the nesting (PERMANOVA, $F=67.6$; $p=0.001$; Figure 6c) and hatching hypervolumes (PERMANOVA, $F=85.1$; $p=0.001$; Figure 6d).

The hypervolume analysis showed that Chichiawan Creek alone contributed 63.3% to the nesting hypervolume, whereas Hehuan Creek contributed 24.0%, with an overlap of only 12.7% (Figure 6c). For the hatching hypervolume, Chichiawan Creek alone contributed 51.6%, whereas Hehuan Creek contributed 33.8%, with an overlap of 14.6% (Figure 6d). These patterns indicate that Chichiawan Creek and Hehuan Creek offer substantial non-overlapping habitat conditions for both nesting and hatching, highlighting the complementary nature of these two creek systems for salmon reproduction.

3.6 | Differential contributions of transects to salmon niche space

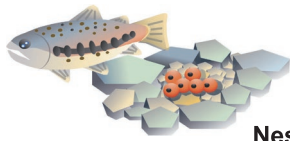
Our transect-level hypervolume analysis revealed that Dam 2 made the largest unique contribution (42.4%) to the nesting hypervolume, with other transects contributing less than 20% each (Figure 6e; Table S5a). In contrast, Hehuan Creek Trail made the largest unique contribution (16.5%) to the hatching hypervolume, with all other transects contributing less than 15% (Figure 6f; Table S5b).

Notably, despite its substantial contribution to the nesting hypervolume, Dam 2 only accounted for 6.0% of the hatching hypervolume (Figure 6f; Table S5b). This suggests that while salmon at this transect use a wide range of conditions for nesting, the environmental conditions that allow for successful hatching generally overlap with those at other transects. In contrast, Hehuan Creek Trail and Wuling Guest House had different environmental conditions that led to varying hatching success rates (Figure 6b,f). Hehuan Creek Trail, with its cooler water temperatures and lower conductivity, produced a high hatch rate (Figure 6b,f). Conversely, Wuling Guest House, with its warmer water temperatures and higher conductivity, had a lower hatching rate (Figure 6b,f).

3.7 | Spatial projection of habitat suitability

To visualize habitat suitability across streams, we mapped the predicted nesting and hatching probabilities and their product based on our Random Forest models, providing an intuitive display of the spatial distribution of habitat suitability in Chichiawan Creek and Hehuan Creek. The results revealed a surprising finding: Hehuan Creek had higher suitability than Chichiawan Creek for both nesting and hatching probability (Figure 7). Specifically, our spatial projections showed that Hehuan Creek had a significantly higher overall nesting probability than Chichiawan Creek (Figure 7a). Hehuan Creek also exhibited significantly higher overall hatching rates, whereas Chichiawan Creek showed high rates only in a small upper reach (Figure 7b). When considering both nesting and hatching rates together, we found that the overall habitat suitability of Hehuan Creek was far superior to that of Chichiawan Creek, with Chichiawan Creek showing slightly higher suitability only in its upstream reaches (Figure 7c). Taken together, these results not only show that the reintroduced Hehuan Creek is indeed more suitable for Formosan

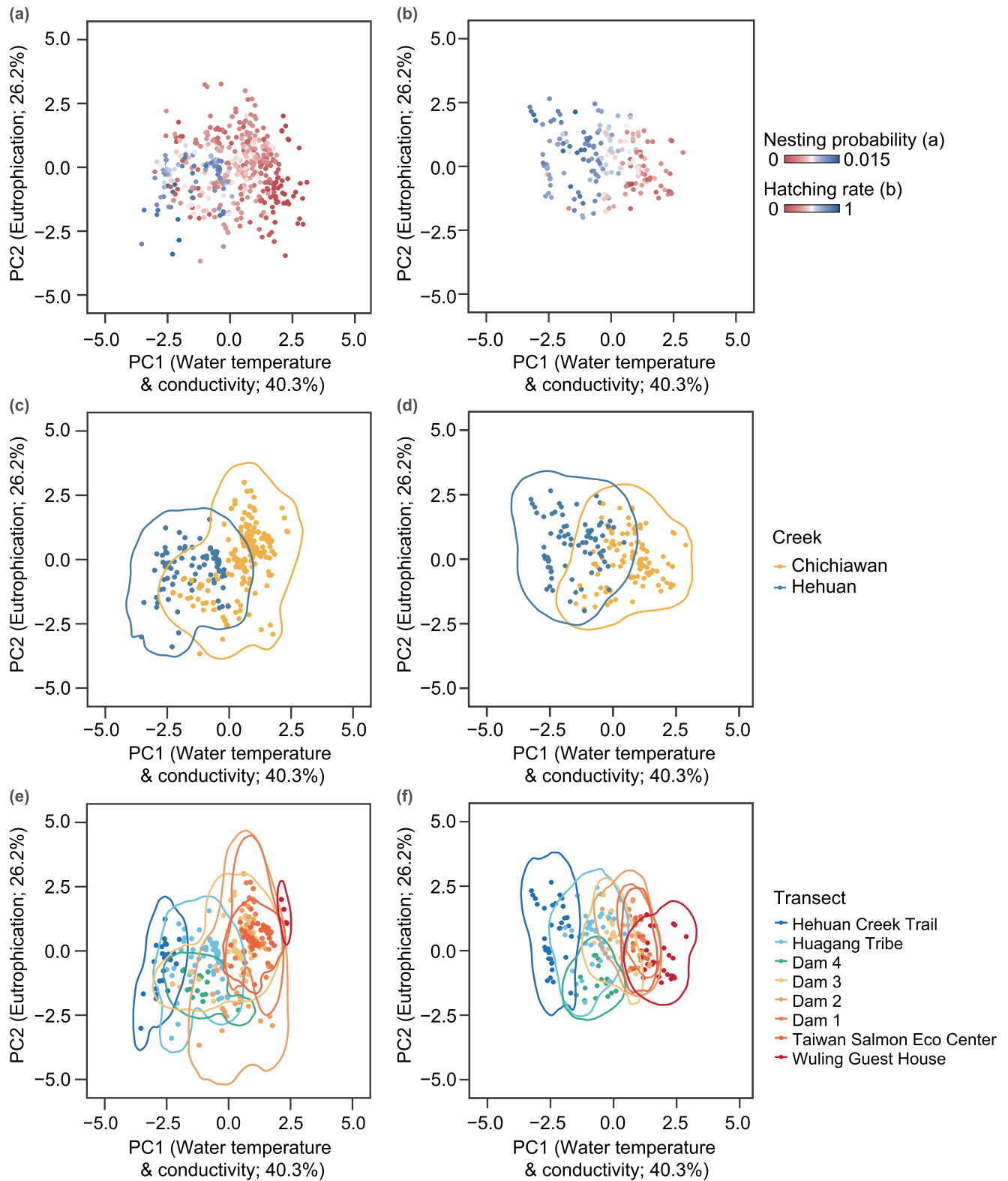
FIGURE 6 Contribution of creeks and sites to nesting and hatching hypervolumes. (a, b) Nesting probability (a) and hatching rate (b) across the environmental space. (c, d) Contribution of each creek to the nesting (c) and hatching (d) hypervolumes. (e, f) Contribution of each site to the nesting (e) and hatching (f) hypervolumes. In (a), points represent both nesting sites and random points, and the colour gradient shows the estimated nesting probability by the product of redd density estimated by GLM and the nest site selection probability estimated by the random forest model, with environmental principal components as predictors. In b, points represent hatching experiment samples, and the colour gradient displays the estimated hatching probability by the random forest model with environmental principal components as predictors. In (c) and (d), different coloured contour lines enclose hypervolumes contributed by different creeks. In (e) and (f), different coloured contour lines enclose hypervolumes contributed by different sites. In (c) and (e), points represent nesting sites. In (d) and (f), points represent hatching experiment samples with an observed hatching rate greater than zero.



Nesting



Hatching



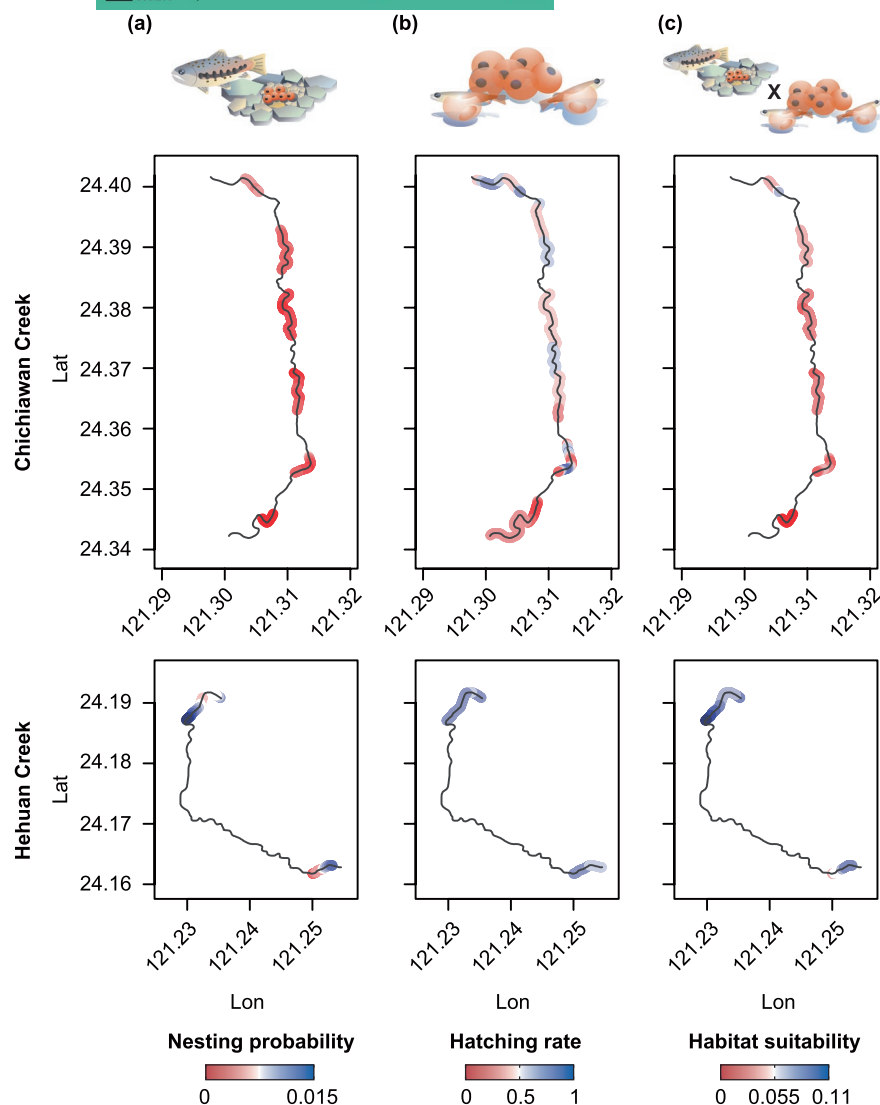


FIGURE 7 Projection of habitat suitability. (a) Nesting probability (product of redd density and nest site selection probability), (b) Hatching rate and (c) Overall habitat suitability (square root of the product of nesting probability and hatching rate). Colour scales indicate the estimated probability or rate. The courses of the creeks are represented by the black line.

landlocked salmon than Chichiawan Creek but also provide important evidence for us to rethink habitat assessment and conservation strategies.

4 | DISCUSSION

Our study provides empirical evidence addressing a fundamental question in conservation biology: Does the habitat of a remnant population truly represent the optimal environment for an endangered species? Our systematic comparison between Chichiawan Creek (a remnant habitat) and Hehuan Creek (a reintroduced historical habitat) yielded three key findings. First, Hehuan Creek provides superior environmental conditions for Formosan landlocked salmon, particularly during the critical hatching stage, with lower water temperatures and conductivity levels that better meet the species' requirements. These differences are especially pronounced during winter reproduction months, highlighting the seasonal dimension of habitat suitability.

Second, our results support the historical narrative documented by Zheng (1987) that overfishing, rather than habitat degradation, was the primary cause of the Formosan landlocked salmon's extinction in Hehuan Creek. By comparing environmental conditions and reproductive success between remnant and reintroduced historical habitats, our approach demonstrates that integrating life stage-specific requirements with habitat comparisons provides more accurate suitability assessments than relying solely on remnant population distributions. This method effectively distinguishes between remnant habitats that represent ecological optima versus those that merely serve as refuges from anthropogenic threats. Our findings align with studies showing that current species distributions may not reflect optimal ecological conditions, as demonstrated in European bison (Kuemmerle et al., 2011), giant kangaroo rats (Rutrough et al., 2019), and other globally extinct and extirpated mammals whose natural ranges were reconstructed (Faurby & Svenning, 2015).

Third, our hypervolume analysis revealed an 'environmental bottleneck' at the egg stage, with hatching requirements being

considerably more stringent than nesting requirements. Using this analysis to quantify the ecological niche for salmon at different life stages, we demonstrated that eggs are particularly sensitive to increases in water temperature and conductivity. These results confirm previous findings on salmonids (Armstrong et al., 2003; Elliott & Elliott, 2010) and align with the broader patterns identified by (Dahlke et al., 2020) regarding the narrower thermal tolerance of embryonic stages, reinforcing the need for multi-stage conservation assessment. Our study also demonstrates complex stage-specific environmental responses in Formosan landlocked salmon. For instance, stream velocity positively affects redd density but negatively impacts nest site selection and hatching rates. Such trade-offs have been documented in desert iguanas (Porter & Tracy, 1983) and California condors (D'Elia et al., 2015), suggesting this phenomenon may be widespread. North American coho salmon (*O. kisutch*) reintroduction projects corroborate our findings, showing that focusing on robust life stages (smolts or adults) can substantially underestimate long-term population viability when early life stages with narrower environmental tolerances are overlooked (Plumb & Perry, 2020). Similarly, Japan's chum salmon (*O. keta*) restoration in Sapporo's Toyohira River provides a particularly relevant parallel, where inadequate early-stage habitats limited population viability despite robust adult returns (Morita & Aruga, 2017). Our hypervolume metrics provide quantitative evidence of niche contraction at the egg stage compared to nesting stages, with implications for understanding evolutionary constraints and adaptation potential.

Although our study was conducted 2–5 years after reintroduction, the reintroduced population was likely beyond the initial establishment phase. This land-locked subspecies matures at 1–2 years of age and rarely survives past 3 years of age, which means that our study covered multiple generations. The strong performance metrics observed at Hehuan Creek, including sustained reproductive success and stable age structure, align with a population transitioning from establishment to growth phase. Recent surveys indicating numerical stabilization and spatial expansion (Liao et al., 2025) suggest successful adaptation to the local environment, though longer-term monitoring would be needed to fully assess population dynamics across varied environmental conditions. These observations, along with the superior habitat conditions that we identified in Hehuan Creek, support our hypothesis that historical local extinctions were primarily driven by overfishing rather than habitat degradation. This finding has implications for reintroduction programs globally, suggesting historical habitats should be reconsidered even when local extinctions occurred decades ago. Collectively, findings from freshwater fishes, including 130 salmonid studies of reintroduction, affirm that success depends on restoring critical environmental parameters—especially for early life stages—while mitigating anthropogenic stressors (Cochran-Biederman et al., 2015).

Based on our findings, we propose specific management implications focused on the identified environmental bottleneck at the egg stage. We recommend that national park authorities implement enhanced protection protocols during the salmon breeding season,

especially during egg hatching from November to December when the species' sensitivity to environmental pollution peaks. Effective strategies may include limiting the number of visitors to campgrounds and hotels near the Chichiawan Stream, and more importantly, strengthening sewage monitoring and regulating sewage discharge to protect critical incubation periods while allowing human activities during less sensitive times. This approach recognizes that complete restriction of human activities is neither practical nor necessary, especially at Wuling Farm where tourism exceeds 250,000 visitors annually. Instead, targeted protection during critical periods offers the greatest conservation return on management investment for Taiwan's Formosan landlocked salmon.

More broadly, our methodological framework advances conservation science by providing a quantitative approach to identifying stage-specific environmental bottlenecks through hypervolume analysis, applicable to other threatened species with complex life cycles. Our findings shift conservation paradigms from static assessments to dynamic, multi-stage evaluations that better capture species' requirements throughout their life cycle. In the context of global environmental change (Pecl et al., 2017), conservation must evolve from protecting individual habitats to preserving species' complete ecological niches (Hanson et al., 2020). While the Kunming-Montreal Global Biodiversity Framework advocates protecting 30% of global land area by 2030 (CBD, 2022), our approach provides scientific criteria for designating protected areas that encompass all critical environments required throughout species' life cycles. By considering both ecological requirements across life stages and historical distributions, and accounting for life stage-specific constraints, minimizing human-driven disturbances and maintaining sufficient genetic diversity, our framework offers a comprehensive approach applicable to other endangered species facing similar challenges, ultimately helping to develop more effective conservation strategies in response to global environmental change. Most importantly, the successful reintroduction of Formosan landlocked salmon to Hehuan Creek challenges the common assumption that remnant habitats represent optimal conditions and highlights the critical importance of distinguishing between habitat degradation and overharvest as causes of local extinctions when planning conservation strategies for endangered species.

AUTHOR CONTRIBUTIONS

Sheng-Feng Shen conceived the ideas and designed methodology; Shih-Fan Chan, Mark Liu, Yi-An Chung, Wei-Ren Lin, Lin-Yan Liao and Sheng-Feng Shen collected the data; Shih-Fan Chan analysed the data; Shih-Fan Chan, Mark Liu, Dustin R. Rubenstein and Sheng-Feng Shen led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the staff of the Wuling Farm of the Veteran Affairs Council, Taiwan, and the Wuling Station of Shei-Pa National Park for logistical support for the field experiments. We also thank Alven Liao, Jou-Hsi

Chen, Shi-Ping Huang and Yu-Hsin Chen for their assistance in the field. S.-F.S. was supported by the Shei-Pa National Park (SP111121).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data and code available via the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.25323022> (Chan et al., 2025).

ORCID

Shih-Fan Chan  <https://orcid.org/0000-0003-2955-9433>

Dustin R. Rubenstein  <https://orcid.org/0000-0002-4999-3723>

Sheng-Feng Shen  <https://orcid.org/0000-0002-0631-6343>

REFERENCES

- Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution*, 23(1), 20–25. <https://doi.org/10.1016/j.tree.2007.10.003>
- Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, 62, 143–170.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, 23, 595–609.
- Blonder, B., Morrow, C. B., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., Enquist, B. J., & Kerkhoff, A. J. (2018). New approaches for delineating n-dimensional hypervolumes. *Methods in Ecology and Evolution*, 9(2), 305–319. <https://doi.org/10.1111/2041-210X.12865>
- Brown, J. H. (1995). *Macroecology*. University of Chicago Press.
- CBD. (2022). *Kunming-Montreal global biodiversity framework: Draft decision submitted by the President*. United Nations Environment Programme Convention on Biological Diversity.
- Chan, S.-F., Liu, M., Rubenstein, D. R., Chung, Y.-A., Lin, W.-R., Liao, L.-Y., & Shen, S.-F. (2025). Data from: Assessment across life stages reveals superior habitat suitability in reintroduced historical habitats for an endangered salmon species. *Figshare*, <https://doi.org/10.6084/m9.figshare.25323022>
- Channell, R., & Lomolino, M. V. (2000). Dynamic biogeography and conservation of endangered species. *Nature*, 403, 84–86.
- Chung, L.-C., Lin, H.-J., Yo, S.-P., Tzeng, C.-S., & Yang, C.-H. (2007). Stage-structured population matrix models for the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in Taiwan. *Raffles Bulletin of Zoology*, 14, 151–160.
- Cochran-Biederman, J. L., Wyman, K. E., French, W. E., & Loppnow, G. L. (2015). Identifying correlates of success and failure of native freshwater fish reintroductions. *Conservation Biology*, 29, 175–186.
- Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, 369, 65–70.
- D'Elia, J., Haig, S. M., Johnson, M., Marcot, B. G., & Young, R. (2015). Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps californianus*). *Biological Conservation*, 184, 90–99.
- Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, 77, 1793–1817.
- Faurby, S., & Svenning, J.-C. (2015). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166.
- Fleming, I. A., Jonsson, B., Gross, M. R., & Lamberg, A. (1996). An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *Journal of Applied Ecology*, 33, 893–905.
- Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., Cowell, C., Weekley, C. W., Vogt, G., Iriando, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjoreke, K., Koopman, R., Vicens, M., Virevaire, M., & Vanderborgh, T. (2011). How successful are plant species reintroductions? *Biological Conservation*, 144, 672–682.
- Hanson, J. O., Rhodes, J. R., Butchart, S. H. M., Buchanan, G. M., Rondinini, C., Ficitola, G. F., & Fuller, R. A. (2020). Global conservation of species' niches. *Nature*, 580, 232–234.
- Iles, D. T., Salguero-Gómez, R., Adler, P. B., & Koons, D. N. (2016). Linking transient dynamics and life history to biological invasion success. *Journal of Ecology*, 104, 399–408.
- IUCN/SSC. (2013). *Guidelines for reintroductions and other conservation translocations*. IUCN/SSC R-Introduction Specialist Group.
- Johnson, D. M. (2004). Source-sink dynamics in a temporally heterogeneous environment. *Ecology*, 85, 2037–2045.
- Kuemmerle, T., Radeloff, V. C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Bashta, A. T., Chikurova, E., Parnikoza, I., Baskin, L., Angelstam, P., & Waller, D. M. (2011). Predicting potential European bison habitat across its former range. *Ecological Applications*, 21, 830–843.
- Lawton, J. H., May, R. M., & Raup, D. M. (1995). *Extinction rates*. Oxford University Press.
- Liao, L.-Y., Chang, C.-Y., & Chiu, H.-Y. (2025). *Population size, distribution, and next year's proposed work for the Formosan landlocked salmon (Oncorhynchus masou formosanus) in Taiwan, 2024*. Shei-Pa National Park Administration & Taroko National Park Administration, Taiwan.
- Liao, L.-Y., Chen, Y.-X., & Chang, C.-Y. (2024). *Population size, distribution, and next year's proposed work for the Formosan landlocked salmon (Oncorhynchus masou formosanus) in Taiwan, 2023*. Shei-Pa National Park Administration & Taroko National Park Administration, Taiwan.
- Liaw, A., & Wiener, M. (2002). Classification and regression by random-forest. *R News*, 2, 18–22.
- Lin, J.-Y., Tsao, E. H., Lee, T.-C., & Yu, S. L. (2004). Stream physical parameters and habitat requirement: The case of the Formosan salmon. *Ecological Engineering*, 22, 305–309.
- Lin, Y., & Chang, K. (1989). Conservation of the Formosan landlocked salmon *Oncorhynchus masou formosanus* in Taiwan, a historical review. *Physiology and Ecology Japan*, 1, 647–652.
- Mayer, M., & Stando, A. (2023). *Shapviz: SHAP visualizations*. R package version 0.9.1.
- Morita, K. (2018). Masu salmon group. In R. J. Beamish (Ed.), *The ocean ecology of Pacific salmon and trout* (pp. 697–702). American Fisheries Society.
- Morita, K., & Aruga, N. (2017). Management procedure for determining the stocking efforts of salmon fry in the Toyohira River: Towards a balance between wild fish conservation and population persistence. *Japanese Journal of Conservation Ecology*, 22, 275–287. (in Japanese).
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., & Minchin, P. (2022). *Vegan: Community ecology package*. R package version 2.6–4.
- Osborne, P. E., & Seddon, P. J. (2012). Selecting suitable habitats for reintroductions: Variation, change and the role of species distribution modelling. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology* (pp. 73–104). Wiley.
- Oshima, M. (1936). Ecological study on the masu of the Taiko River. *Botany and Zoology*, 4, 1–13.

- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214.
- Plumb, J. M., & Perry, R. W. (2020). *Development of a two-stage life cycle model for Oncorhynchus kisutch (coho salmon) in the upper Cowlitz River Basin, Washington*. Open-File Report.
- Porter, W. P., & Tracy, G. R. (1983). Lizard ecology: 3. Biophysical analyses of energetics, time-space utilization, and distributional limits. In R. B. Huey, E. R. Pianka, & T. W. Schoener (Eds.), *Studies of a model organism* (pp. 55–83). Harvard University Press.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, 132, 652–661.
- Pulliam, H. R., & Danielson, B. J. (1991). Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *The American Naturalist*, 137, S50–S66.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R package version 4.2.1. R Foundation for Statistical Computing.
- Robert, A., Colas, B., Guigon, I., Kerbiriou, C., Mihoub, J. B., Saint-Jalme, M., & Sarrazin, F. (2015). Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. *Animal Conservation*, 18, 397–406.
- Rutrough, A., Widick, I. V., & Bean, W. T. (2019). Reconstruction of the historical range alters niche estimates in an endangered rodent. *Ecography*, 42, 1742–1751.
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, 345, 406–412.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.
- Walters, C. (1997). Challenges in adaptive management of riparian and coastal ecosystems. *Conservation Ecology*, 1(2), 1–16.
- Whitlock, D. (1977). *The Whitlock Vibert box handbook*. Federation of Fly Fishermen.
- Yackulic, C. B., Sanderson, E. W., & Uriarte, M. (2011). Anthropogenic and environmental drivers of modern range loss in large mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 4024–4029.
- Zheng, M.-N. (1987). *Final report on the ecological survey of Formosan landlocked salmon and alpine fish, Natural Resources in Taroko National*

Park. Construction and Planning Agency, Ministry of the Interior. https://npda.nps.gov.tw/files/27/12427/pta_1687_2985478_07519.pdf. (in Chinese)

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Materials & methods details.

Table S1: PCA loadings of environmental variables.

Table S2: The influence of environmental factors on redd density of the Formosan landlocked salmon.

Table S3: The influence of environmental factors on nest site selection of the Formosan landlocked salmon.

Table S4: The influence of environmental factors on hatching rate of the Formosan landlocked salmon.

Table S5: The contribution of each transect to the (a) nesting and (b) hatching hypervolumes.

Figure S1: Nesting and hatching hypervolumes of the Formosan landlocked salmon.

Figure S2: Effect sizes of environmental factors and transects on salmon nest site selection.

Figure S3: Effect sizes of environmental factors and transects on salmon hatching rate.

How to cite this article: Chan, S.-F., Liu, M., Rubenstein, D. R., Chung, Y.-A., Lin, W.-R., Liao, L.-Y., & Shen, S.-F. (2025). Assessment across life stages reveals superior habitat suitability in reintroduced historical habitats for an endangered salmon species. *Journal of Applied Ecology*, 62, 1378–1391. <https://doi.org/10.1111/1365-2664.70067>