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Contributed Paper

Identifying correlates of success and failure of native freshwater fish reintroductions

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Abstract: *Reintroduction of imperiled native freshwater fish is becoming an increasingly important conservation tool amidst persistent anthropogenic pressures and new threats related to climate change. We summarized trends in native fish reintroductions in the current literature, identified predictors of reintroduction outcome, and devised recommendations for managers attempting future native fish reintroductions. We constructed random forest classifications using data from 260 published case studies of native fish reintroductions to estimate the effectiveness of variables in predicting reintroduction outcome. The outcome of each case was assigned as a success or failure on the basis of the author's perception of the outcome and on whether or not survival, spawning, or recruitment were documented during post-reintroduction monitoring. Inadequately addressing the initial cause of decline was the best predictor of reintroduction failure. Variables associated with habitat (e.g., water quality, prey availability) were also good predictors of reintroduction outcomes, followed by variables associated with stocking (e.g., genetic diversity of stock source, duration of stocking event). Consideration of these variables by managers during the planning process may increase the likelihood for successful outcomes in future reintroduction attempts of native freshwater fish.*

Keywords: native fish, population supplementation, program evaluation, random forests, reintroduction, translocation

Identificación de Correlaciones de Éxito y Fracaso de Reintroducciones de Peces de Nativos Agua Dulce

Resumen: *La reintroducción de peces nativos de agua dulce que se encuentran en peligro se está convirtiendo cada vez más en una herramienta importante de conservación frente a las presiones antropogénicas persistentes y nuevas amenazas relacionadas con el cambio climático. Resumimos las tendencias encontradas en la literatura actual sobre la reintroducción de peces nativos, identificamos pronosticadores de resultados de la reintroducción e ideamos recomendaciones para administradores que intenten reintroducciones de peces nativos en el futuro. Construimos clasificaciones de bosque aleatorio a partir de datos de 260 estudios de caso publicados sobre la reintroducción de peces nativos para estimar la efectividad de las variables en la predicción del resultado de la reintroducción. El resultado de cada caso fue asignado como un éxito o un fracaso con base en la percepción del autor a partir del resultado y dependiendo de si se documentó o no la supervivencia, el desove o el reclutamiento durante el monitoreo posterior a la reintroducción. Abordar inadecuadamente a la causa inicial de la declinación fue el mejor pronosticador del fracaso de la reintroducción. Las variables asociadas con el hábitat (p. ej.: calidad del agua, disponibilidad de la presa) también fueron buenos pronosticadores de los resultados de la reintroducción, seguidas por las variables asociadas con el stock (p. ej.: la diversidad genética de la fuente del stock, duración del evento de stock). Que los administradores consideren estas variables durante el proceso de planeación puede incrementar la probabilidad de resultados exitosos en futuros intentos de reintroducción de peces nativos de agua dulce.*

Palabras Clave: bosques aleatorios, complementación de la población, peces nativos, programa de evaluación, reintroducción, translocación

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Introduction

Biodiversity has been closely linked to ecosystem productivity, stability, and quality of ecosystem services (Tilman 1999; Worm et al. 2006; Pejchar & Mooney 2009). Consequently, biodiversity loss is a primary concern of ecologists worldwide, particularly in the case of freshwater ecosystems (Sala et al. 2000; Olson et al. 2002; Dudgeon et al. 2006). Although comprising only 0.01% of global water supply and 0.8% of Earth's surface, freshwater ecosystems support approximately 5% of all described species and 43% of described fish species (Helfman 2007; Grosberg et al. 2012). Because they support a disproportionately high number of species and are more vulnerable to biodiversity loss than terrestrial or marine systems, freshwater ecosystems are a priority for conservation (Dudgeon et al. 2006).

Freshwater fish populations are vulnerable to a host of threats (e.g., overexploitation, habitat loss, invasive species) that may act in concert to reduce or eliminate populations (Clausen & York 2008; Lyons et al. 2010; Woodward et al. 2010). Key strategies for restoring freshwater fish populations include habitat restoration, removal of invasive species, and supplementation via translocation or stocking of hatchery-reared individuals (Harig et al. 2000; Shute et al. 2005; Schooley & Marsh 2007). Although these methods aim to strengthen the viability of existing populations, managers are increasingly faced with situations where a native fish has been extirpated from part of its historical range, leaving reintroduction as the only option for restoring the presence and functionality of the species in the ecosystem.

In response to the growing use of reintroduction as a management tool (Armstrong & Seddon 2008), broad guidelines have been developed for conservation-based reintroductions, including those offered by the International Union for the Conservation of Nature Species Survival Commission (2013). These guidelines offer a detailed framework for all stages of reintroductions, generalized for all plant and animal taxa. Because reintroduction efforts involving aquatic ecosystems present unique challenges, specific guidelines for fish reintroductions have also been developed (Williams et al. 1988; Meffe 1995; Dunham et al. 2011).

Although these guidelines have likely contributed to the successful recovery of threatened fish populations, there has been no comprehensive review of completed reintroductions to identify specific factors associated with success, as has been done for plant and other animal taxa (Griffith et al. 1989; Fischer & Lindenmayer 2000; Godefroid et al. 2011). The identification of such factors has the potential to improve existing fish reintroduction frameworks for better outcomes. Because native fish reintroductions can be costly, often requiring captive rearing, repeated stockings, and extensive monitoring, high likelihood of a successful outcome can increase the willingness of stakeholders and decision makers to devote limited resources to reintroduction efforts. Thus, our goals were to summarize trends and effectiveness of native freshwater fish reintroductions within the current literature; identify predictors of perceived reintroduction success or failure and predictors of survival and reproduction of reintroduced individuals; and provide recommendations for managers attempting native fish reintroductions in the future.

Methods

Literature Review

We used search terms related to native freshwater fish reintroduction to locate reports of completed reintroduction efforts in 6 databases: Aquatic Sciences and Fisheries Abstracts (ProQuest); Fish, Fisheries & Aquatic Biodiversity Worldwide (EBSCO); Google Scholar; Web of Science (Thomson Reuters); Wildlife & Ecology Studies Worldwide (EBSCO); and Zoological Record (ProQuest). Our search was limited to publicly available studies published in English. Studies retained for analysis described reintroduction of a native freshwater fish where the intent was to establish a population and evaluated reintroduction success with a post-reintroduction monitoring period of ≥6 months. These criteria yielded 75 studies published between 1989 and 2013, including peer-reviewed literature and reports from governmental and nongovernmental agencies (Supporting Information). The studies contained 260 individual cases of fish reintroduction. Each case was distinguished as a separate event based on unique species, location, or method. When multiple studies reported on the same reintroduction, we combined data reported in each paper to yield a more complete picture of the case.

Data Collected and Definitions

Information recorded for each case included species introduced and associated life history characteristics, type and size of freshwater system, reintroduction location, year of first fish release, and publication year. We used these data to describe the scope of the literature review, and some data were included in the analysis to determine their relationship to reintroduction outcome (Table 1 & Supporting Information).

The authors' determinations of reintroduction outcome (success or failure) were identified in each case study; however, authors' definitions of success and failure varied according to the unique goals or objectives of each study. To conduct a more objective analysis, we also identified 3 binary biological indicators of outcome: survival (whether or not reintroduced fish were found alive ≥6 months after reintroduction), spawning (whether or not

Table 1. Names and descriptions of variables that may contribute to success or failure of a reintroduction effort.

Variable name	*Type*	*Description*
Species characteristic		
Game	binary	commercial or sport-fishing value of species
Migratory	binary	reproductive strategy (potamodromous, anadromous, or catadromous)
Age of maturity	continuous	age of first reproduction
Spawning guild	categorical	broadcast spawning, host symbiosis, parental care, or substrate specificity
Temperature guild	binary	warm water (daily maximum average temperature >22 °C) or cold water (daily maximum average temperature <22 °C)
Protected	binary	official governmental protection status at time of reintroduction
Stocking mechanics		
Stock source	binary	wild or hatchery
Remnant	binary	presence of remnant population of the species at reintroduction site
Number stocked	continuous	number of individuals stocked over the course of reintroduction
Oldest stocked	ordinal	oldest fish stocked as adults, juveniles, fingerlings, or fry and younger
Years stocked	continuous	number of years stocking occurs
Local adaptation	binary	adaption of source stock to local conditions
Genetic diversity	binary	source stock genetically diverse
Reintroduction site		
Addressed cause of decline	binary	original cause of population decline or extirpation identified and considered resolved prior to reintroduction
Non-native present	binary	presence of non-native fish species
Hab assessed	binary	reintroduction site assessed for suitability prior to reintroduction
Repro hab available	binary	spawning and nursery habitat available
Water quality	binary	adequate water quality
Prey	binary	sufficient prey
Habitat type	binary	reintroduction in a riverine or a lacustrine environment
Habitat size	ordinal	spatial scale of the reintroduction*
Social factors		
Mult stakeholder	binary	multiple stakeholder participation in reintroduction effort
Financial support	binary	project has sufficient financial support

[a] *Variable had the following levels: 1, < 1000 cfs (mean annual; riverine) or <100 ha (lacustrine); 2, 1000–9999 cfs (riverine) or 100–999 ha (lacustrine); 3, ≥10,000 cfs (riverine) or ≥ 1000 ha (lacustrine).*

reintroduced fish were observed to spawn after reaching sexual maturity), and recruitment (whether or not the offspring of reintroduced fish were observed to join the breeding population).

Finally, factors that might contribute to success or failure of a reintroduction were documented for each case study (Table 1). These factors were chosen a priori based on a preliminary review of the reintroduction literature and the authors' knowledge of fish biology. To ensure consistency in interpretation, 2 reviewers independently scored each case study for the variables under consideration. Discrepancies were resolved collaboratively.

Statistical Analyses

We used chi-square tests of independence to measure the degree of association between authors' definitions of success and biological measures of success (survival, spawning, recruitment). We used Wald significance tests to assess the relationship between length of the post-reintroduction monitoring period and probability of a positive reintroduction outcome (author-defined or biological measures).

We evaluated the relative importance of predictor variables in predicting reintroduction outcome using a conditional random forest algorithm implemented in party (Hothorn et al. 2006*a*; Strobl et al. 2007; Strobl et al. 2008) in program R (R Core Team 2012). Random forests are a valuable tool for classifying cases according to a binary outcome because no data must be excluded for accuracy testing later, they are robust to outliers and noise, they lack distributional assumptions, and they are able to handle problems where the ratio of number of cases to number of predictor variables (n:p) is low (Breiman

2001; Cutler et al. 2007). The use of conditional inference trees as components of the forest reduces variable selection bias when both continuous and categorical variables are present (Strobl et al. 2009). The algorithm ran with 3000 trees to stabilize variable importance measures and with 5 covariates in the selection pool at each node. We calculated each variable's importance in predicting outcome according to the method of Hapfelmeier and colleagues (2014). This method calculates the increase in the misclassification rate when the algorithm's optimal division of cases among child nodes for a variable of interest is replaced with random allocation of cases to child nodes. The larger the increase in the misclassification rate, the more important the variable is for correct classification of the response (Breiman 2001). Because studies did not always report covariates of interest, missing covariate values were assigned using "surrogate" splits (Hothorn et al. 2006*b*). Covariate values were available for >70% of case studies for all but one predictor (prey) (Table 1).

We evaluated the ability of the random forest to discriminate between reintroduction failure and success using the area under the receiver operating characteristic curve (AUC), which ranges from 0.5, for a classifier that is no better than random, to 1.0, for a perfect classifier (Hanley & McNeil 1982). Initial AUC values fell well below 0.5, indicating that the classifier was predicting failure (initially represented as 0) much more accurately than success (1). Switching the value used to indicate failure to 1 and the value used to indicate success to 0 brought the AUC values into the expected range; thus, the reported results focus on the relationship between predictors and reintroduction failure.

Results

Among 260 case studies of native freshwater fish reintroductions drawn from the published literature, 149 attempts (58%) were successful and 109 were unsuccessful (42%) by the authors' definitions. In 2 cases, authors judged the outcome to be inconclusive. Survival of reintroduced fish was assessed in >99% of cases, spawning in 87% of cases, and recruitment in 70% of cases.

Fifty-two species from 14 families were represented; 27 species carried commercial value (60% of cases) and 15 species were migratory (20% of cases). Most reintroductions took place in North America (75%), followed by Asia (12%) and Europe (12%). A majority of reintroductions occurred in riverine habitats (60%) and on smaller spatial scales (75% in streams with mean annual discharge rates of <28.3 cm or lakes with surface areas of <100 ha).

Definitions of Success and Failure

There were strong associations between author-defined success of a reintroduction effort and confirmation of survival ($\chi^2 = 62.1$, df = 1, $p < 0.0001$), spawning ($\chi^2 = 95.2$, df = 1, $p < 0.0001$), and recruitment ($\chi^2 = 99.1$, df = 1, $p < 0.0001$) among reintroduced fish. Both survival and recruitment of reintroduced fish were documented in 86% of cases that were classified as successful. No authors classified an effort as successful without documenting survival. *Failure* was more broadly defined across studies. Sixteen cases in which both survival and recruitment were documented were considered failures. There was no relationship between the length of time spent monitoring a reintroduction and its perceived success ($z = -0.09$, df = 243, $p = 0.93$) or between the length of the monitoring and observations of survival ($z = 1.01$, df = 244, $p = 0.32$), spawning ($z = -0.10$, df = 210, $p = 0.92$), or recruitment ($z = -0.11$, df = 168, $p = 0.91$).

Predictors of Reintroduction Outcome

Across all species, addressing the cause of a population's initial decline (variable addressed cause of decline [i.e., identifying the cause of population decline and confirming the resolution of the problem through monitoring or restoration]) was strongly associated with author-defined and reproductive outcomes of reintroduction (Figs. 1a–d). Sixty-five percent of failed cases did not address the initial cause of decline, whereas over 68% of successful cases did. Because many predictors in the analysis could be a cause of decline (e.g., presence of non-native species, inadequate water quality), we repeated the analysis without the variable addressed cause of decline (Figs. 1e–h). Removal of this variable did not substantially change the relative importances of remaining variables in predicting reintroduction outcome.

Confirming the presence of physical habitat at the reintroduction site (habitat assessment) was the most important action to avoid spawning failure, and it reduced the likelihood of recruitment failure and author-defined failure (Fig. 1). Several other aspects of reintroduction site quality also figured into survival and reproductive failures (Fig. 1). Presence of non-native fishes at the reintroduction site was an important predictor of author-defined failure, but not of biological outcomes (Fig. 1).

Stocking variables were somewhat less important than reintroduction site characteristics in predicting reintroduction failure, but several were among the top 5 predictors in one or more random forest classifications (Fig. 1). Use of locally sourced broodstock and stocking over a long period (local adaptation and years stocked) were important in preventing mortality of the reintroduced population (Figs. 1b & 1f). Among the cases examined, 71% of recruitment failures and 77% of author-defined failures were associated with hatchery-reared fish.

As a group, intrinsic species characteristics affected reintroduction outcome the least. Migratory species

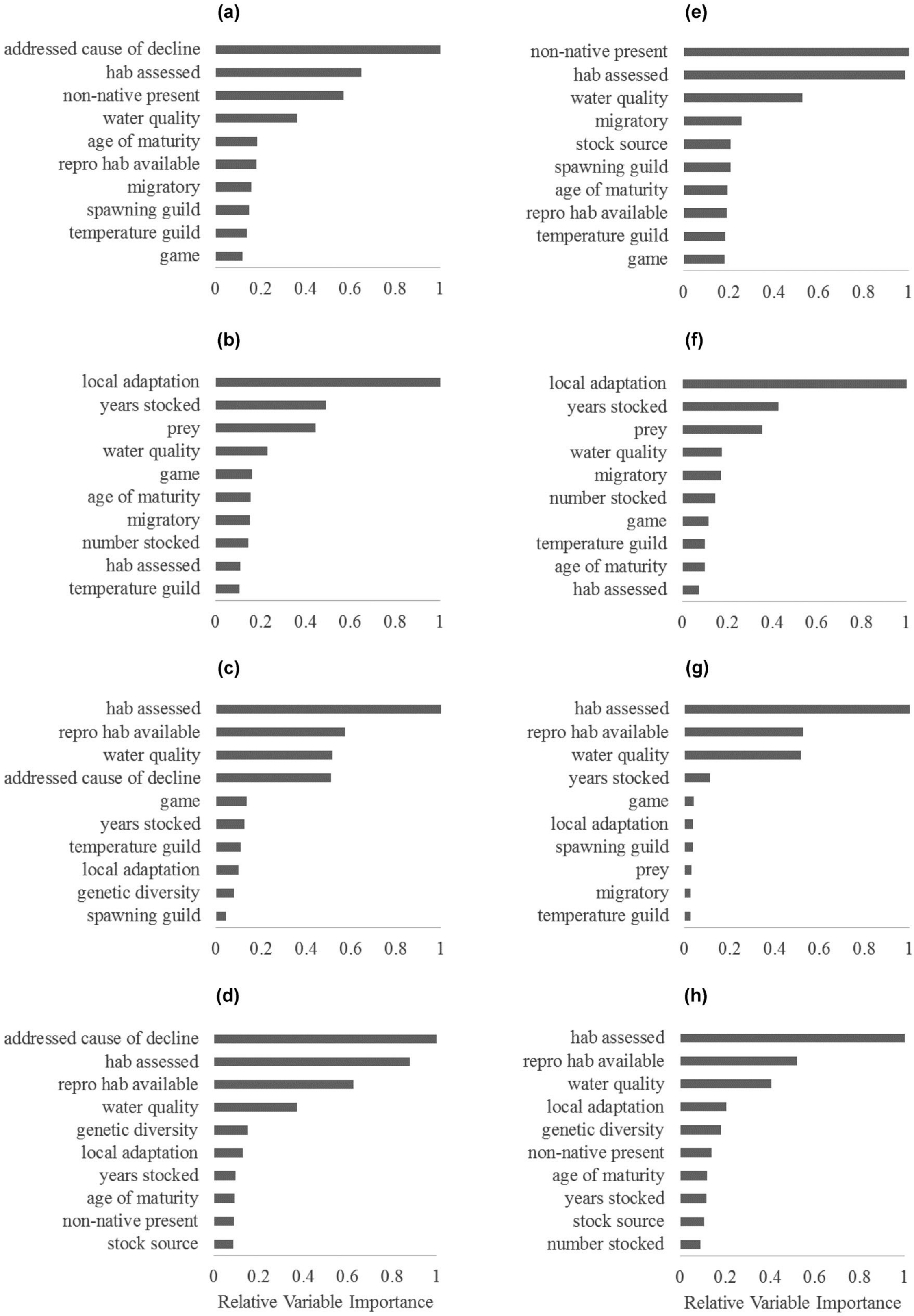

Figure 1. Ten most important variables in random forest classifications of (a, e) author-defined failure and (b, f) failures of survival, (c, g) spawning, and (d, h) recruitment on reintroductions of all freshwater fish species pooled (0.0, least effect; 1.0, most effect). In a–d the variable cause of decline was included, whereas in e–h it was not. Variable definitions are in Table 1.

more commonly survived for ≥6 months after reintroduction than nonmigratory species (94% vs. 83%). Although it did not predict reproductive failures, spawning guild affected prediction of author-defined failures. All 8 cases of species exhibiting parental care as a reproductive strategy succeeded, whereas cases involving other guilds (broadcast spawners [$n = 56$], host symbionts [$n = 12$], and substrate-specific spawners [$n = 177$]) were perceived as failures in 40–50% of cases.

Because half of cases (130 cases) involved species in the family Salmonidae, additional random forest classifications were constructed for salmonids and nonsalmonids separately (Fig. 2). Neither analysis addressed the cause of decline as a predictor variable due to overlap of this variable with other predictors. Salmonid results differed considerably from nonsalmonid results, but for both groups, reintroduction site characteristics and stocking variables were more influential than species characteristics. Protected status was the only species trait that had a strong relationship with author-defined reintroduction outcome: reintroduction attempts of nonsalmonids with governmental protection were more prone to failure than those without protection (Fig. 2e). Migratory life history was an important predictor of salmonid survival; migratory species survived at slightly higher rates (survival in 97% of cases) than nonmigratory species (survival in 93% of cases).

Among reintroduction site characteristics, prereintroduction habitat assessment (habitat assessment) remained important in differentiating failures from successes in salmonid reintroductions (Figs. 2a, c, & d). However, water quality was the most influential site characteristic in nonsalmonid reintroductions; inadequate water quality was linked to lack of survival, spawning, and recruitment (Figs. 2f–h).

Genetic features of the source stock (genetic diversity and local adaptation) rose in importance as predictors of mortality, recruitment failure, and author-defined failure in both salmonids and nonsalmonids in the split analyses. Salmonids had higher survival when the source stock was adapted to local conditions. Spawning failure in nonsalmonids and recruitment failure in both groups occurred more often with use of genetically diverse stocks. The age of the oldest individuals stocked also became important in the split analyses; the proportion of cases exhibiting recruitment failure decreased monotonically as age of the oldest individuals stocked increased (Figs. 2c & 2d).

Classifiers ably discriminated both author-defined and biological failures from successes on the basis of AUC values, which ranged from 0.84 to 0.91. All classifiers would be considered excellent (AUC > 0.8) predictors of reintroduction failure under the framework of Hosmer and Lemeshow (2000).

Discussion

Measurement of Reintroduction Success

The strong associations we found between author-defined success and observations of survival and reproduction reinforce the perception that these are popular benchmarks for success. Survival and reproduction are central to the goal of most reintroduction programs, which is to establish a self-sustaining population (Robinson & Ward 2011). However, reintroduction efforts commonly have more nuanced goals, such as a particular rate of survival or population growth, that are too variable to have been included in this broad analysis. For example, failure was declared in some cases because of the presence of non-native species or inadequate population growth (Harig et al. 2000; Wu et al. 2008), despite survival and reproductive success. The time frame over which success or failure is judged is also important; lack of observed reproduction even after several years of monitoring may not be sufficient to signal reintroduction failure in long-lived species.

Based on author-defined success, the ratio of successes to failures in the 260 reintroduction attempts included in this analysis was biased toward successes (58% and 42%, respectively). Successes are likely to have a higher publication rate than failures because authors desire to inform others of factors that led to reintroduction success and to portray involved parties favorably. A review of translocations of herpetofauna in New Zealand reported that the rate of success for published projects was much higher than the rate of success for all translocations, and successful projects were more likely to be published than failed projects or those with uncertain outcomes (Miller et al. 2014). Similarly, a review of the success of animal reintroductions showed that 47% of published case studies were considered successful, but the authors believed failures were underreported (Fischer & Lindenmayer 2000). Thus, the sample of published failures in our analysis may be a small fraction of all failed reintroductions. Furthermore, although the number of publications related to native fish reintroductions increased substantially between 1989 and 2013 (Supporting Information), it is realistic to assume that many reintroductions are not reported in the literature. Thus, it seems reasonable to conclude that the results of our analysis are representative of the available literature, but perhaps not of all fish reintroductions.

Environmental Variables

Identifying and addressing the initial cause of decline is one of the most important actions to take to avoid reintroduction failure. This contention is supported by our results with native freshwater fish and by published work for other taxa (Fischer & Lindenmayer 2000). The strength of the association between addressing the initial

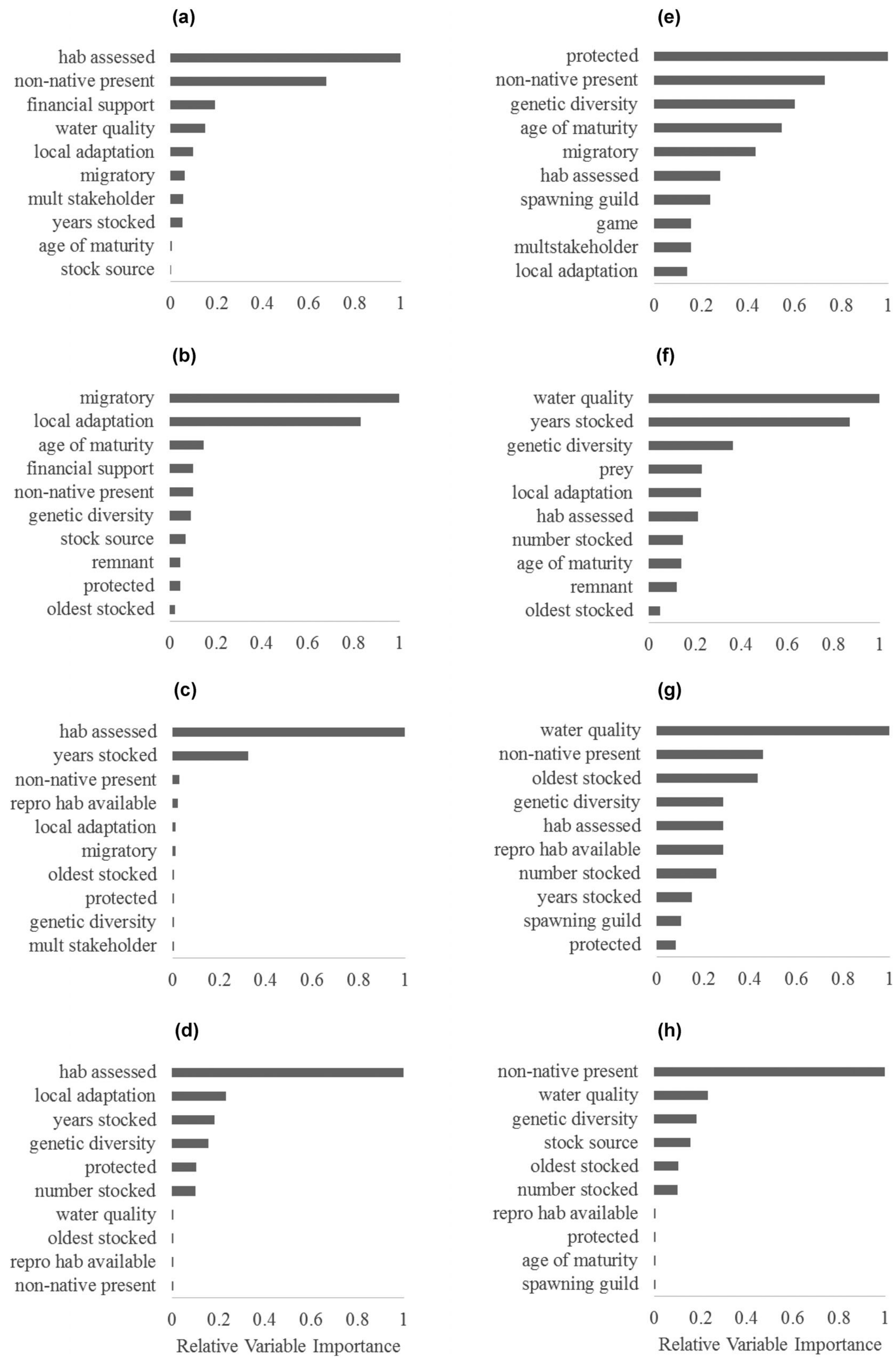

Figure 2. Ten most important variables in random forest classifications of (a) author-defined failure and (b) failures of survival, (c) spawning, and (d) recruitment for salmonid reintroductions versus (e) author-defined failure and (f) failures of survival, (g) spawning, and (h) recruitment for nonsalmonid reintroductions. Variable definitions are in Table 1.

cause of decline and failure suggests that managers should carefully research which factors led to declines in the species they plan to reintroduce. Because factors leading to species loss can be multifaceted, complex, or difficult to identify, it may be equally important to confirm that factors suspected of contributing to the initial cause of decline have been addressed. Reintroduction plans should be tailored to address issues specific to the species and location in order to improve their odds of success.

Presence of non-native species at a reintroduction site can threaten survival, growth, and reproduction of reintroduced fish through both competition for resources and predation (Al-Chokhachy et al. 2009; Impson 2011). Presence of non-native species was an important predictor of author-defined failure for all species (Fig. 1) and of reproductive failures in non-salmonids (Fig. 2). The importance of non-native species to authors' assessment of outcome may have been driven by authors' chosen success criteria because non-native species was not an important predictor of most biological outcomes (Harig et al. 2000; Mukai et al. 2011). Invasive species are a serious threat to biodiversity, second only to habitat loss (Walker & Steffen 1997). The minor effect of non-native fish on most biological outcomes we found is puzzling, but it may be due to the diversity of species, habitats, and life histories we considered.

Biophysical variables, especially the presence of reproductive habitat, were important predictors of reintroduction outcomes. Without spawning and nursery habitat, a population cannot reproduce and establish (Monnerjahn 2011). Habitat assessments have been strongly recommended to help managers select reintroduction sites containing necessary habitat for reintroduced species to complete their lifecycles (Williams et al. 1988; Dunham et al. 2011). Most studies identified the selection of reintroduction site as an important contributing factor to subsequent reintroduction outcome (e.g., Burt 2007; Goren 2009). If habitat was not available at the reintroduction site, authors often described ongoing habitat restoration efforts (Philippart et al. 1994; Kirschbaum et al. 2011; Monnerjahn 2011). To improve the odds of reintroduction success, all life history stages should be supported by suitable biophysical conditions (e.g., substrate, water quality, prey availability) in the reintroduction sites selected during the planning process.

Stocking Variables

In general, stocking variables were less powerful predictors of reintroduction failure than environmental variables. Among salmonids in particular, stocking fish from a locally adapted source reduced mortality in reintroduced populations. Genetic diversity of source stock had moderate importance among outcomes for both salmonids and nonsalmonids; less diverse stocks typically exhibited stronger reintroduction outcomes. The literature supports the importance of population genetics for reintroduction success and highlights the problems of inbreeding and outbreeding depression that can come from improper choice of source stocks (Leberg 1993; Gum et al. 2009; Moyer et al. 2009; Sousa et al. 2010; Huff et al. 2011). Choice of appropriate genetic composition of stock can be complicated because there are many factors to consider including rarity, ecological compatibility, geographic location, and genetic diversity (Minckley 1995; Weeks et al. 2011). Despite this complexity, it appears that managers realize the potential importance of genetics to the ultimate success of reintroduction attempts because 225 of the 260 cases examined reported accounting for genetic diversity or local adaptation in choosing reintroduction stock.

Although most stocking variables were only moderately important in predicting reintroduction failure, years of stocking ranked among the top predictors of mortality for reintroductions of all species and of spawning and recruitment failure among salmonids. This result suggests that repeated stocking improves establishment probability, as has been found in other studies (Hilderbrand 2002; Sheller et al. 2006). If fish are stocked annually for several years, they may be more likely to encounter a favorable year for survival or reproduction (Lyon 2012). Population modeling of cutthroat trout (*Onchorhynchus clarki*) shows that stocking in multiple years can compensate for other stocking practices (e.g., low number stocked, small size of stocked fish) that might otherwise reduce probability of population persistence (Hilderbrand 2002). Longer reintroduction programs may also indirectly indicate more effort and resources available, which could improve the odds of success.

Intrinsic Species Characteristics

Although each predictor included in the analysis was expected to influence reintroduction success, intrinsic characteristics of the reintroduced species were not particularly significant. The exception to this trend was that government-protected status was the top predictor of overall failure in nonsalmonid reintroductions. Species with protected status at the time of reintroduction may have characteristics that make them inherently more susceptible to extinction, including naturally small distributions and a high degree of ecological specialization (Angermeier 1995).

Overall, however, the results suggest that the species being reintroduced is less important to success than the habitat chosen for the reintroduction. Given the presence of habitat and adequate stocking practices, the fish should survive and reproduce. These results contrast somewhat with the findings of reviews of reintroductions in other taxa, which have identified both environmental characteristics and species characteristics as important predictors of reintroduction success (Griffith et al. 1989; Fischer

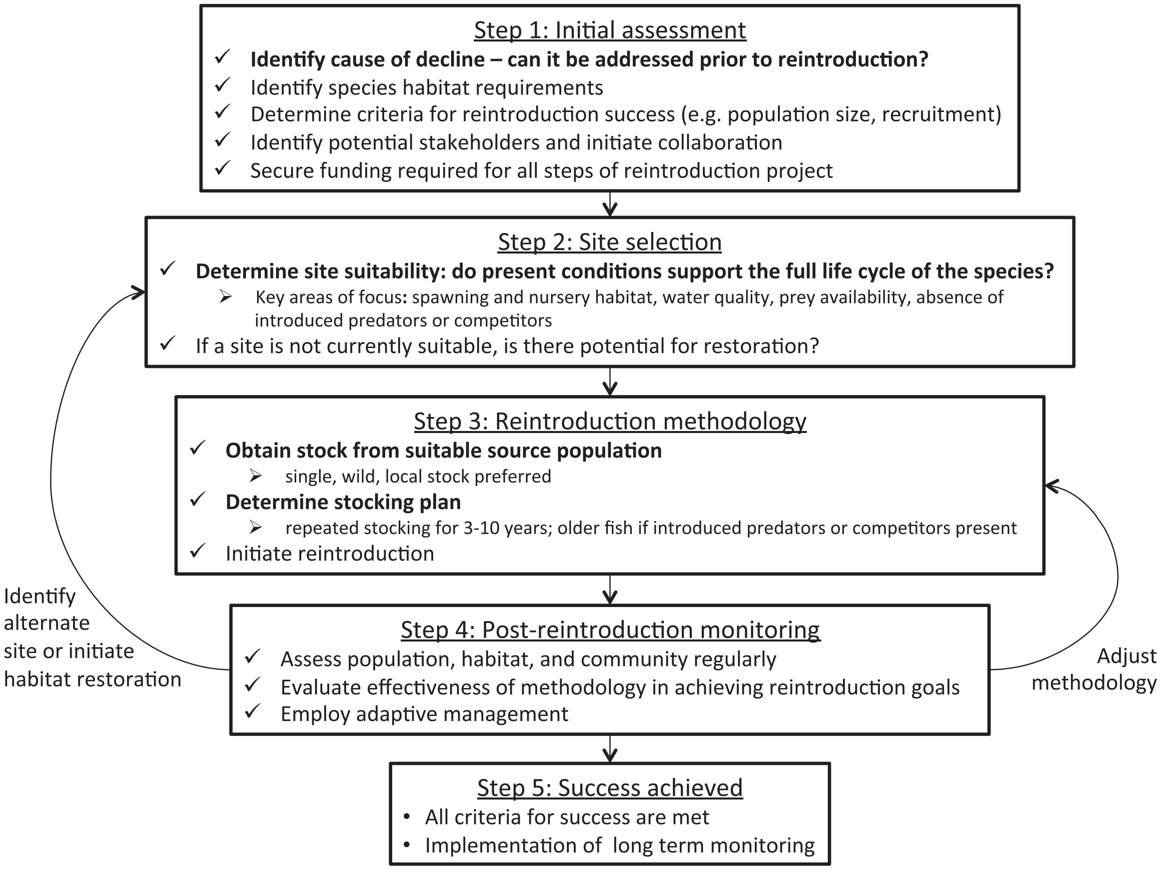

Figure 3. Recommended process for native freshwater fish reintroductions. Actions with strong influence on reintroduction outcomes are in bold.

& Lindenmayer 2000; Godefroid et al. 2011). However, of these only Godefroid et al. (2011) used a multivariate analysis to compare relative importance of predictors as we did, and the majority of significant variables in their study were also environmental.

Recommendations for Future Reintroductions

Although broad reintroduction guidelines for plant and animal taxa exist (Williams et al. 1988; Meffe 1995; IUCN/SSC 2013), native freshwater fish reintroductions may require a more specific framework. We identified key variables that potentially influence outcomes of native freshwater fish reintroductions, which may help managers design and deploy more successful reintroduction efforts in the future.

Our results suggest that environmental variables (e.g., suitable biophysical conditions, availability of spawning and rearing habitat) and to a lesser extent stocking variables (e.g., quantity and frequency of stockings, size of stocked individuals) have important associations with reintroduction outcomes. We recommend that managers consider these aspects at each step of the reintroduction process when planning and implementing reintroduction attempts within specific systems (Fig. 3).

Although environmental variables are not always easy to manipulate, managers should focus on addressing them because these are the variables most strongly related to reintroduction outcome. By selecting sites that have not been affected by the initial cause of species decline, contain few or no non-native species, and provide adequate habitat, managers can improve the odds of reintroduction success. If ideal sites do not exist, attempts to create more suitable sites through management actions (e.g., non-native species removal or control, habitat improvement projects, etc.) may improve reintroduction outcome (Kitazima et al. 2011; Mukai et al. 2011). Knowledge of current habitat requirements and cause of species decline will be valuable information for managers during this process, and pre-reintroduction assessments should be conducted (Dunham et al. 2011).

Stocking variables are more easily manipulated by managers and can have a moderate impact on reintroduction outcome. Managers may be able to partially compensate for suboptimal environmental conditions through manipulation of stocking variables. Stocking practices must be carefully selected for each situation based on knowledge of the species in question and the system in which the reintroduction will occur (Hilderbrand 2002). Genetics should also be considered when selecting stocks for a reintroduction attempt (Frankham 1995; Frankham 2005; Weeks et al. 2011), and salmonid reintroductions should place particular emphasis on obtaining locally adapted stock.

Finally, identification of appropriate success criteria, involvement of multiple stakeholders, and acquisition of sufficient funding can be important aspects of a successful reintroduction attempt, particularly if they influence a program's ability to use suitable reintroduction sites and stocking practices (Shute et al. 2005; Kitazima et al. 2011). Although our results did not show that involvement of stakeholders is directly tied to reintroduction outcome, resolution of conflicts among stakeholders may be necessary to address the initial cause of population decline (Wu et al. 2008; Ingendahl et al. 2010). Similarly, financial concerns did not carry much predictive weight, but lack of adequate funding could influence a program's ability to conduct full habitat assessments, remove non-native species, or stock adequate numbers or sizes of fish (Harig et al. 2000; Al-Chokhachy et al. 2009; Impson 2011). The ultimate goal of a reintroduction attempt should be the establishment of a self-sustaining population. Accordingly, in addition to being an important step toward gaining knowledge to improve future reintroduction efforts, long-term monitoring of reintroduced populations is an important component of a successful reintroduction program (Schram et al. 1999; Zymonas 2011). Long-term monitoring is required to detect changes in population trajectory occurring after active reintroduction has ceased and may improve success via the application of adaptive management techniques (Bearlin et al. 2002).

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Supporting Information

A reference list of 85 peer-reviewed articles and reports from which case studies were drawn (Appendix S1) and case study summary data (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of materials) should be directed to the corresponding author.

Literature Cited

Al-Chokhachy, R., M. Peacock, L. G. Heki, and G. Thiede. 2009. Evaluating the reintroduction potential of Lahontan cutthroat trout in Fallen Leaf Lake, California. North American Journal of Fisheries Management **29:**1296–1313.

Angermeier, P. L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conservation Biology **9:**143–148.

Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. Trends in Ecology & Evolution **23:**20–25.

Bearlin, A. R., E. S. G. Schreiber, S. J. Nicol, A. Starfield, and C. R. Todd. 2002. Identifying the weakest link: simulating adaptive management of the reintroduction of a threatened fish. Canadian Journal of Fisheries and Aquatic Sciences **59:**1709–1716.

Breiman, L. 2001. Random forests. Machine Learning **45:**5–32.

Burt, A. 2007. Brook trout reintroduction: Lake Erie Drainage, NE Ohio. Report no. F3SM02. Ohio Department of Natural Resources, Division of Wildlife, Columbus, Ohio.

Clausen, R., and R. York. 2008. Global biodiversity decline of marine and freshwater fish: a cross-national analysis of economic, demographic, and ecological influences. Social Science Research **37:** 1310–1320.

Cutler, D. R., T. C. J. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology **88:**2783–2792.

Dudgeon, D., et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews **81:** 163–182.

Dunham, J., K. Gallo, D. Shively, C. Allen, and B. Goehring. 2011. Assessing the feasibility of native fish reintroductions: a framework applied to threatened bull trout. North American Journal of Fisheries Management **31:**106–115.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation **96:**1–11.

Frankham, R. 1995. Conservation genetics. Annual Review of Genetics **29:**305–327.

Frankham, R. 2005. Stress and adaptation in conservation genetics. Journal of Evolutionary Biology **18:**750–755.

Godefroid, S., et al. 2011. How successful are plant species reintroductions? Biological Conservation **144:**672–682.

Goren, M. 2009. Saving critically endangered fish species – utopia or a practical idea? The story of the Yarqon bleak – *Acanthobrama telavivensis* (Cyprinidae). Aqua, International Journal of Ichthyology **15:**1–12.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245:**477–480.

Grosberg, R. K., G. J. Vermeij, and P. C. Wainright. 2012. Biodiversity in water and on land. Current Biology **22:**900–903.

Gum, B., R. Gross, and J. Geist. 2009. Conservation genetics and management implications for European grayling, *Thymallus thymallus*: synthesis of phylogeography and population genetics. Fisheries Management and Ecology **16:**37–51.

Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology **143:**29–36.

Hapfelmeier, A., T. Hothorn, K. Ulm, and C. Strobl. 2014. A new variable importance measure for random forests with missing data. Statistics and Computing **24:**21–34.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management **20:**994–1004.

Helfman, G. S. 2007. Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington, D.C.

Hilderbrand, R. H. 2002. Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. North American Journal of Fisheries Management **22:**879–887.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd ed. Wiley, New York.

Hothorn, T., P. Buehlmann, S. Dudoit, A. Molinaro, and M. Van Der Laan. 2006*a*. Survival ensembles. Biostatistics **7:**355–373.

Hothorn, T., K. Hornik, and A. Zeileis. 2006*b*. Unbiased recursive partitioning: a conditional inference framework. Journal of Computational and Graphical Statistics **15:**651–674.

Huff, D. D., L. M. Miller, C. J. Chizinski, and B. Vondracek. 2011. Mixed-source reintroductions lead to outbreeding depression in second-generation descendents of a native North American fish. Molecular Ecology **20:**4246–4258.

Impson, N. D. 2011. Re-introduction of endangered Berg-Breede whitefish to the upper Berg River in the Western Cape Province of South Africa. Pages 15–19 in P. S. Soorae, editor. Global re-introduction perspectives: 2011. More case studies from around the globe: IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi, Gland, Switzerland and Abu Dhabi, UAE.

Ingendahl, D., H. Klinger, F. Molls, and A. Nemitz. 2010. Re-introduction of Atlantic salmon to the river Rhine system: case study of the river Sieg, Germany. Pages 53–57 in P. S. Soorae, editor. Global re-introduction perspectives: additional case-studies from around the globe. IUCN/ SSC ReIUCN/ SSC Re-introduction Specialist Group, Abu Dhabi, UAE.

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. Version 1.0. IUCN Species Survival Commission, Gland, Switzerland.

Kirschbaum, F., P. Williot, F. Fredrich, R. Tiedemann, and J. Gessner. 2011. Restoration of the European sturgeon *Acipenser sturio* in Germany. Pages 309–333 in P. Williot, E. Rochard, N. Desse-Berset, F. Kirschbaum, and J. Gessner, editors. Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758: The Reunion of the European and Atlantic Sturgeons. Springer-Verlag, New York, New York.

Kitazima, J., S. Takeda, M. Matsuda, S. Nishida, and S. Mori. 2011. Translocation and re-introduction project of striped bitterling in Lake Biwa and neighboring areas, Japan. Pages 59–64 in P. S. Soorae, editor. Global re-introduction perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi, Gland, Switzerland and Abu Dhabi, UAE.

Leberg, P. L. 1993. Strategies for population reintroduction: effects of genetic variability on population growth and size. Conservation Biology **7:**194–199.

Lyon, J. P. 2012. Reintroduction success of threatened Australian trout cod (*Maccullochella macquariensis*) based on growth and reproduction. Marine Freshwater Research **63:**598–605.

Lyons, J., J. S. Stewart, and M. Mitro. 2010. Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, U.S.A. Journal of Fish Biology **77:**1867–1898.

Meffe, G. K. 1995. Genetic and ecological guidelines for species reintroduction programs: application to Great Lakes fishes. Journal of Great Lakes Research **21:**3–9.

Miller, K. A., T. P. Bell, and J. M. Germano. 2014. Understanding publication bias in reintroduction biology by assessing translocations of New Zealand's herpetofauna. Conservation Biology **28:**1045–1056.

Minckley, W. L. 1995. Translocation as a tool for conserving imperiled fishes: experiences in western United States. Biological Conservation **72:**297–309.

Monnerjahn, U. 2011. Atlantic salmon (*Salmo salar* L.) re-introduction in Germany: a status report on national programmes and activities. Journal of Applied Ichthyology **27:**33–40.

Moyer, G. R., J. Rousey, and M. Cantrell. 2009. Genetic evaluation of a conservation hatchery program for reintroduction of sicklefin redhorse *Moxostoma sp.* in the Tuckasegee River, North Carolina. North American Journal of Fisheries Management **29:**1438–1443.

Mukai, T., K. Tsukahara, and Y. Miwa. 2011. The re-introduction of the Ushimotsugo minnow in Gifu Prefecture, Japan. Pages 54–58 in P. S. Soorae, editor. Global re-introduction perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi, Gland, Switzerland and Abu Dhabi, UAE.

Olson, D. M., E. Dinerstein, G. V. N. Powell, and E. D. Wikramanayake. 2002. Conservation biology for the biodiversity crisis. Conservation Biology **16:**1–3.

Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology & Evolution **24:**497–504.

Philippart, J. C., J. C. Micha, E. Baras, C. Prignon, A. Gillet, and S. Joris. 1994. The Belgian project "Meuse Salmon 2000": first results, problems, and future prospects. Water Science and Technology **29:**315–317.

R Core Team. 2012. R: a language and environment for statistical computing, Version 2.15.1. R Foundation for Statistical Computing, Vienna.

Robinson, A. T., and D. L. Ward. 2011. Interactions between desert pupfish and Gila topminnow can affect reintroduction success. North American Journal of Fisheries Management **31:**1093–1099.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the Year 2100. Science **287:**1770–1774.

Schooley, J. D., and P. C. Marsh. 2007. Stocking of endangered razorback suckers in the Lower Colorado River Basin over three decades: 1974–2004. North American Journal of Fisheries Management **27:**43–51.

Schram, S. T., J. Lindgren, and L. M. Evrard. 1999. Reintroduction of Lake Sturgeon in the St. Louis river, Western Lake Superior. North American Journal of Fisheries Management **19** (3): 815–823.

Sheller, F. J., W. F. Fagan, and P. J. Unmack. 2006. Using survival analysis to study translocation success in the Gila topminnow (*Poeciliopsis occidentalis*). Ecological Applications **16:**1771–1784.

Shute, J. R., P. L. Rakes, and P. W. Shute. 2005. Reintroduction of four imperiled fishes in Abrams Creek, Tennessee. Southeastern Naturalist **4:**93–110.

Sousa, V., F. Penha, I. Pala, L. Chikhi, and M. Coelho. 2010. Conservation genetics of a critically endangered Iberian minnow: evidence of population decline and extirpations. Animal Conservation **13:**162–171.

Strobl, C., A. L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. Conditional variable importance for random forests. BMC Bioinformatics **9:**307.

Strobl, C., A. L. Boulesteix, A. Zeileis, and T. Hothorn. 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. BMC Bioinformatics **8:**25.

Strobl, C., T. Hothorn, and A. Zeileis. 2009. Party on! A new, conditional variable-importance measure for random forests available in the party package. The R Journal **1:**14–17.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology **80:** 1455–1474.

Walker, B., and W. Steffen. 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. Conservation Ecology **1**(2).

Weeks, A. R., et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications **4:**709–725.

Williams, J. E., D. W. Sada, and C. D. Williams. 1988. American Fisheries Society guidelines for introductions of threatened and endangered fishes. Fisheries **13:**5–11.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences **365:**2093–2106.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314:**787–790.

Wu, H. C., K. C. Lee, and P. F. Lee. 2008. Restoration of the formosan landlocked salmon in the Shei-Pa National Park, Taiwan. Pages 42–46 in P. S. Soorae, editor. Global re-introduction perspectives: re-introduction case-studies from around the globe. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE.

Zymonas, N. D. 2011. Re-introduction of bull trout in the upper Willamette River basin, USA. Pages 44–48 in P.S. Soorae, editor. Global re-introduction perspectives: more case studies from around the globe. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE.