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# Prioritizing ecological restoration among sites in multi-stressor landscapes

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*Abstract.* Most ecosystems are impacted by multiple local and long-distance stressors, many of which interact in complex ways. We present a framework for prioritizing ecological restoration efforts among sites in multi-stressor landscapes. Using a simple model, we show that both the economic and sociopolitical costs of restoration will typically be lower at sites with a relatively small number of severe problems than at sites with numerous lesser problems. Based on these results, we propose using cumulative stress and evenness of stressor impact as complementary indices that together reflect key challenges of restoring a site to improved condition. To illustrate this approach, we analyze stressor evenness across the world's rivers and the Laurentian Great Lakes. This exploration reveals that evenness and cumulative stress are decoupled, enabling selection of sites where remediating a modest number of high-intensity stressors could substantially reduce cumulative stress. Just as species richness and species evenness are fundamental axes of biological diversity, we argue that cumulative stress and stressor evenness constitute fundamental axes for identifying restoration opportunities in multi-stressor landscapes. Our results highlight opportunities to boost restoration efficiency through strategic use of multi-stressor datasets to identify sites that maximize ecological response per stressor remediated. This prioritization framework can also be expanded to account for the feasibility of remediation and the expected societal benefits of restoration projects.

*Key words: cumulative impact; fresh water; prioritization; restoration; stressor interactions; synergy.*

## Introduction

Restoration of degraded ecosystems is an increasingly important component of conservation efforts, complementing the preservation of wild places (Dobson et al. 1997). Global spending on restoration is growing rapidly and includes over US$1 billion per year spent on river restoration projects in the USA alone (Bernhardt et al. 2007). As these investments grow, it is important to ensure that resources are targeted effectively. There have been repeated calls for a better understanding of the costs and benefits of restoration (Kondolf 1995, Bash and Ryan 2002, Palmer et al. 2005, Bernhardt and Palmer 2007), as well as the sociopolitical challenges of implementing restoration plans (Light and Higgs 1996, Hobbs 2004, Hobbs 2007), yet methods for prioritizing restoration investments have not yet addressed multi-stressor landscapes (Beechie et al. 2008, McBride et al. 2010, Holl and Aide 2011, Wilson et al. 2011).

Many of the key challenges in prioritizing restoration projects stem from the fact that most ecosystems are impacted by multiple local and global stressors, which often interact in complex and little-understood ways (Crain et al. 2008, Darling and Côté 2008). The implications of this are threefold. First, single-stressor restoration efforts may have little real benefit if they fail to account for the remaining problematic stressors at a site (Evans et al. 2011, Allan et al. 2013). Second, when stressors interact, the ecosystem response to the remediation of a particular stressor will depend on how that stressor interacts with co-occurring stressors (Crain et al. 2008, Darling and Côté 2008, Brown et al. 2013). Third, the economic and sociopolitical costs of remediating any one stressor may vary among sites depending on the presence of other co-occurring stressors, even when these stressors themselves have no mechanistic interactions (Evans et al. 2011, Wilson et al. 2011). As a result, certain combinations of stressors may lead to opportunities for economic efficiency (e.g., logistical savings via shared equipment and personnel costs), thereby lowering the cost of restoration. In other cases, combinations of stressors may lead to conflicts among stakeholders who differ in their assessment of the costs and benefits of restoration projects.

Spatial analyses of cumulative stress or impact (CS) are increasingly embraced as a means of summarizing a host of ecosystem impairments (Danz et al. 2007, Halpern et al. 2008, Vörösmarty et al. 2010, Allan et al. 2013,

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Halpern and Fujita 2013). Integrating multiple stressors into a single index provides a straightforward summary of ecosystem stress, which enables practitioners to focus their efforts toward a particular level of CS if desired. For instance, some organizations focus on protecting areas that are in a relatively pristine state, while others actively seek to restore areas that are already heavily degraded (Game et al. 2008, Ban et al. 2010, Vörösmarty et al. 2010). While cumulative stress ratings can streamline initial prioritization, large-scale analyses still identify far more potential intervention locations with equivalent CS than it would be feasible to restore. Furthermore, decision makers may mistakenly interpret CS ratings as a prioritization (Tulloch et al. 2015); in reality, indices of CS do not give any indication of how the practical challenges of restoration efforts vary among the many sites with equivalent stress ratings (Brown et al. 2013), nor do they give a full indication of the ecological benefits of remediating a site. Thus, it would be desirable to derive further insight into restoration opportunities from multi-stressor datasets than is provided by CS alone.

In multi-stressor landscapes, both economic and sociopolitical costs are key practical constraints on restoration success (O'Connor et al. 2003, McBride et al. 2007, Joseph et al. 2009, Faleiro and Loyola 2013) and both types of costs may depend in complex ways on the suite of stressors at a site. For example, dam removals are an increasingly common strategy for restoring aquatic connectivity, but the cost of a dam removal often depends on whether there are co-occurring stressors, like invasive species and contaminated impounded sediments, which would be exacerbated by removing that dam (Stanley and Doyle 2003). In that context, the cost of removing contaminated sediments and controlling invasive species must be considered as part of the dam removal cost. At the same time, conflicts among stakeholders may be driven by stressor interactions in a way that is not reflected in the economic costs of a dam removal (Jórgensen and Renöfält 2013). In the North American Great Lakes, for example, dam removals are often contentious because they have the potential to facilitate the spread of invasive species and may allow migratory fishes to serve as vectors for pathogens and contaminants (McLaughlin et al. 2013). Conflicts over the ecological costs and benefits of dam removal are often severe, but do not have an obvious resolution because they are rooted in the contrasting mandates and value systems of different stakeholders (Kueffer and Kaiser-Bunbury 2013). In the case of dams, then, consideration of only the economic cost, or only the sociopolitical cost of removal, would likely result in a poor estimate of the true practical challenges of a project.

We develop and analyze a framework for understanding how the economic and sociopolitical costs of ecological restoration might vary among sites with equivalent cumulative stress in multi-stressor ecosystems. Though we focus on understanding restoration costs, our approach could readily be adapted to also consider various societal and ecological benefits of restoration. For example, ecosystem remediation can be carried out to enhance ecosystem services (Palmer and Filoso 2009), to protect biodiversity across a suite of species (Auerbach et al. 2014) or particular beneficiary species, or to address organizational mandates to remediate a particular stressor or class of stressors. Our framework is equally applicable across the full cumulative stress spectrum, allowing the prioritization of restoration among sites at any level of overall impairment. Based on our analysis of idealized models, we propose a heuristic metric of the practical challenges of restoring a site to improved condition. To explore potential applications of this approach, we apply this metric to cumulative stress data for the world's rivers and the Great Lakes to identify locations where restoration may be most feasible.

## Models and Analysis

We first define key terms and then introduce three general classes of functions that describe the relationships between stressor intensity and the costs of restoration. We then analyze these functions in a series of increasingly complex scenarios: a two-stressor landscape with no interactions among stressors, a two-stressor landscape with interactions, and then a multi-stressor landscape with diverse stressor interactions and divergent cost functions. Though simple, our initial two-stressor scenarios provide the foundation of the final, multi-stressor scenario.

### *Definitions*

Consider a group of $I$ sites or regions that are candidates for restoration. Each site $i$ has a vector of $N$ stressors $X_{i.}$ Each element $X_{i,n}$ describes the intensity or severity of stressor $n$ at site $i$. We assume that intensities for all stressors have been converted to a standard scale (e.g., a continuous value ranging from zero to one; Allan et al. 2013). This normalization process puts otherwise incommensurable stressors (e.g., invasive species and heavy metal contamination of sediments) into comparable units based on expected ecological importance and provides a standardized scale for measuring improvements in ecosystem condition resulting from remediation (Halpern and Fujita 2013).

The economic cost of remediating a stressor to improved condition is given by a cost function, which describes the cost of reducing the intensity of stressor $n$ at site $i$ to some target level of lower intensity, $T_{i,n}$:

$$\phi_{i,n}\left(X_{i,n} - T_{i,n}\right).$$

In this formulation, the cost of restoring stressor $n$ at $i$ is calculated independently for each stressor. This is appropriate for sites with only a single stressor, but for sites with multiple stressors, we must account for the possibility that the presence of other stressors will increase or decrease the cost of remediating $i$. To do this, we define a new cost function describing the cost of remediating stressor $n$ at $i$ given the other stressors that must also be remediated at that site:

$$\phi_{i,n}\left(X_{i,n}-T_{i,n},X_{i,-n}\right).$$

Here $x_{i-n}$ denotes the vector describing the intensities of stressors other than $n$. In this formulation, the cost of remediating a stressor may be more or less expensive, relative to sites where it occurs alone, depending on what other remediation is occurring at the site. We define synergy as the potential savings in economic cost, at site $i$, for stressor $n$ when all other stressors are also restored.

$$S_{i,n}=\phi_{i,n}\left(X_{i,n}-T_{i,n}\right)-\phi_{i,n}\left(X_{i,n}-T_{i,n},X_{i,-n}\right).$$

Synergy is a fundamental concept in our model; it describes how the cost of remediating a stressor will depend on the set of other stressors at a site. Synergies can be positive or negative. The set of stressors $-n$ creates an opportunity for positive synergy when the cost of restoring stressor $n$ is lowered relative to sites where it occurs alone. This might occur, for example, when a set of stressors can all be remediated using the same personnel and equipment, so that these costs can be shared among stressors; or when the remediation of stressors $-n$ would diminish the intensity of stressor $n$ (i.e., a synergistic stressor interaction) and thus the cost of remediating it. Conversely, the set of stressors $-n$ can lead to negative synergy when the cost of remediating stressor $n$ is higher than at sites where it occurs alone. This will primarily occur via antagonistic stressor interactions, where the remediation of stressors $-n$ increases the intensity of stressor $n$. Dams and invasive species are a case in point; the cost of removing a dam is typically higher at sites with the potential to harbor invasive species (because of subsequent control costs) than at sites where dams occur without invasive species.

Because the term $\phi_n\left(X_{i,n}-T_{i,n},X_{i,-n}\right)$ accounts for any interactions among stressors, the total cost of restoring site $i$ is the summation of these terms over all $N$ stressors, $Cost_i=\sum_{n=1}^{N}\phi_{i,n}\left(X_{i,n}-T_{i,n},X_{i,-n}\right)$. The total potential savings due to synergies at site $i$ is the summation of $S_{i,n}$ across all $N$ stressors, $S_i=\sum_{n=1}^{N}S_{i,n}$.

This framework can also be applied to understanding the sociopolitical costs of restoration. In this case, we focus upon the human dimensions of launching, coordinating, and completing restoration projects. Accordingly, we define sociopolitical cost in the broadest possible sense to encompass all social and political aspects of restoration. As with economic synergies, sociopolitical synergies are a fundamental concept in our model because they describe how the sociopolitical cost of remediating a stressor will depend on the other stressors at a site. The set of stressors $-n$ creates an opportunity for positive synergy when the sociopolitical cost of restoring stressor $n$ is lowered relative to sites where that stressor occurs alone. This can occur, for example, among stressors that can be remediated using similar expertise, regulatory permissions, or existing collaborations among agencies. Where these stressors co-occur, sociopolitical costs can be shared among stressors. Conversely, the set of stressors $-n$ leads to negative synergy when the sociopolitical cost of restoring $n$ is higher at sites with $-n$ than at sites where $n$ occurs alone. This can occur when the remediation of one stressor exacerbates another, and stakeholders differ in their valuation of these two stressors. Dams and invasive species are a case in point: dam removal can allow invasive species to spread further in a watershed, and dam removals are often contentious because stakeholders differ in their valuation of ecological benefits vs. ecological costs (e.g., facilitating species invasions). Consequently, the sociopolitical cost of dam removal is typically higher at sites with both dams and invasive species than at sites where dams occur without risk of species invasions.

### *Classes of cost functions*

Nearly all restoration cost functions will belong to one of three classes (Fig. 1). The first class includes any function where the cost is constant and independent of stressor intensity (Type I, Fig. 1). This class of functions likely describes the sociopolitical dimension of most restoration projects: there will be a set of sociopolitical challenges (engaging experts, aligning stakeholders, regulatory hurdles, etc.) that will be incurred regardless of

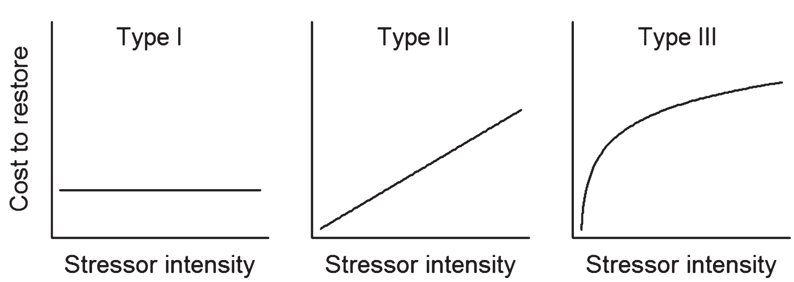


FIG. 1. Three general classes of cost functions, which relate the cost of restoring a stressor (vertical axis) to the intensity of that stressor (horizontal axis).

the severity of the stressor. The second class includes any function in which cost increases linearly with stressor intensity. This might describe, for example, the cost of controlling an invasive plant species via manual application of herbicide (e.g., as with *Phragmites*; Farnsworth and Meyerson 1999), where the total cost of restoration increases roughly linearly with the total amount of herbicide used and the number of person-hours needed to apply it. The third and perhaps most common class includes any function in which cost is a strictly increasing but concave-down function of stressor intensity. This class of functions describes cases where highly degraded sites are only marginally more expensive to restore. Such cases are likely to be common because economies of scale should apply to restoring highly degraded sites. For example, economies of scale are known to exist for groundwater remediation (Sutherland et al. 2005), PCB mitigation (Woodyard 1990), the removal of heavy metals from soils (Jelusic and Lestan 2014) and the management costs of nature reserves (Armsworth et al. 2011). By definition, Type III functions exhibit the mathematical property of being strictly and globally subadditive (i.e., $\phi\left(X_1+X_2\right)<\phi\left(X_1\right)+\phi(X_2)$).

Super-additive cost functions (i.e., concave-up), in which heavily degraded sites have an increased cost of remediation per unit of stressor intensity (i.e., a diseconomy of scale), are likely to be rare because they can arise in only two ways. First, when severely degraded sites require categorically different and more expensive remediation methods than less degraded sites, the restoration cost per unit of stressor intensity may be higher for the most degraded sites. For example, moderate amounts of acid mine drainage may be mitigated using low-cost wetland treatment systems (Sheoran and Sheoran 2006), but more costly treatment methods are required for the more heavily degraded sites. Second, when an invasive species or pathogen has a very rapid rate of growth or spread, it may be more costly to control in regions where it is well established due to the likelihood of reinvasion. For example, eradication of an invasive species may be possible and relatively inexpensive where that species is at low density, but costly suppression strategies may be needed for well-established invaders (Myers et al. 2000).

### *Scenario I: Two stressors, no synergies*

The simplest multi-stressor restoration scenario is a landscape with two stressors, no stressor synergies ($S_i = 0$ at all sites), and no differences in the cost functions among sites and between stressors. Each site in this landscape has an identical level of cumulative stress (i.e., $X_{i,1} + X_{i,2}$ equal for all *i* sites), but sites differ in the degree to which the intensity of one stressor is greater than the intensity of the other (i.e., degree of stressor heterogeneity; Fig. 2A). For two sites A and B with equivalent CS, site A has higher stressor heterogeneity than B if $X_{A,1} > X_{B,1}$ and $X_{A,2} < X_{B,2}$.

In this and all following scenarios, we assume that the goal is to reduce all stressors to some target intensity *T*. Thus, we simplify the notation hereafter by writing the cost function $\phi_n\left(X_{i,n}-T_{i,n}\right)$ as simply $\phi_n\left(X_{i,n}\right)$. In the case where restoration targets vary significantly among stressors, conclusions are by definition less general, so we focus on scenarios where the target stressor intensity is comparable.

In this simple scenario, it is always preferable to work at sites with high stressor heterogeneity. If cost follows either a Type I or Type II function, the cost of remediation depends only on the number of stressors that must be addressed. As a result, sites with a single stressor will always be less costly than sites with two stressors. For Type III functions, we can make use of the subadditivity in the cost function to show that, in this simple scenario, there is a perfect negative correlation between stressor heterogeneity and the cost of restoration. For two sites where site A has higher stressor heterogeneity than site B (i.e., $X_{A,1} > X_{B,1}$ and $X_{A,2} < X_{B,2}$), if the cost function is subadditive (e.g., as in Type III), then

$$\phi_{A,1}\left(X_{A,1}\right)+\phi_{A,2}\left(X_{A,2}\right)<\phi_{B,1}\left(X_{B,1}\right)+\phi_{B,2}\left(X_{B,2}\right) \quad (1)$$

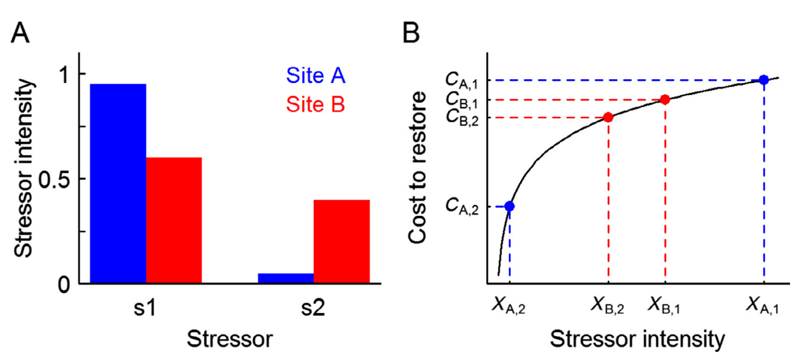


FIG. 2. For subadditive cost functions, sites with high stressor heterogeneity are less expensive to restore. (A) Hypothetical patterns of stressor intensity in a simple landscape of two sites A and B each with two stressors (s1, s2). Sites A and B have equivalent cumulative stress ($X_{A,1} + X_{A,2} = X_{B,1} + X_{B,2}$), but site A has higher stressor heterogeneity. (B) Due to subadditivity in the cost function (solid line), site A is less expensive to restore (i.e., $C_{A,1} + C_{A,2} < C_{B,1} + C_{B,2}$).

Eq. 1 dictates that it will always be less expensive to restore site A than site B. This result is an outcome of the mathematical property of subadditivity in Type III cost functions and is illustrated graphically in Fig. 2B. Note that for super-additive functions, which we hypothesize to be rare, the opposite conclusion arises: it will always be preferable to work at sites with low stressor heterogeneity, because high intensity stressors would be disproportionately costly to remediate.

### *Scenario II: Two stressors with synergies*

We again consider a landscape with two stressors, but now allow for synergies among the two stressors at a site (i.e., $S_i \neq 0$). When these two stressors have negative synergies ($S_i < 0$), sites where both stressors occur will carry an additional cost that is not shared by sites with only one stressor. As a result, negative synergies among stressors will always reinforce the findings in the previous scenario, i.e., it will remain preferable to work at sites with high stressor heterogeneity. When these two stressors exhibit positive synergies ($S_i > 0$), sites where both stressors occur will present an opportunity for lowered costs that is not present at sites with only a single stressor. Whether this reverses the conclusion in the previous scenario will depend on the magnitudes of synergies: when synergies are large, they may reverse the inequality in Eq. 1. In that case, it will be preferable to work at sites with two stressors rather than one because the marginal cost of addressing the second stressor is low given restoration effort toward the first.

### *Scenario III: A multi-stressor landscape*

In realistic multi-stressor landscapes, the cost of restoring a site to improved condition will typically be a complex function of the number and intensity of stressors at that site, their individual cost functions, and synergies among these stressors. We conducted a series of simulation experiments to explore how the correlation between cost and stressor heterogeneity might depend on this complex set of factors. We simulated landscapes in which each site had identical cumulative stress and the same number of stressors, but the intensity of each stressor varied among sites. We modeled synergies between stressors as random draws from a normal distribution with mean of zero and variable standard deviation ($\sigma$). We assumed that all stressors but one followed the same cost function; the exceptional stressor was considered more costly to restore by a linear factor $z$ per unit stressor intensity. Each simulation yielded an estimate of total cost to restore a site, reflecting both direct costs of remediating the set of stressors (hereafter "base cost") and costs arising from stressor synergies. For details, see Appendix S1.

As a first experiment, we manipulated $\sigma$ to explore how synergy strengths affect the correlation between restoration cost and stressor heterogeneity. When synergies were small relative to the base cost, the total cost of restoring a site (i.e., base cost plus synergies) was highly correlated with stressor evenness (Fig. 3A). As synergies increased in magnitude, the correlation between the total cost of restoration and stressor evenness declined, eventually approaching zero when the standard deviation of synergies was larger than the base cost of restoring a site. In other words, stressor heterogeneity is a reliable metric of overall cost when synergies among stressors are small, but an unreliable metric when synergies are so large that they are the primary determinants of restoration cost.

As a second experiment, we manipulated $z$ to explore how differences in the costs of restoring stressors might

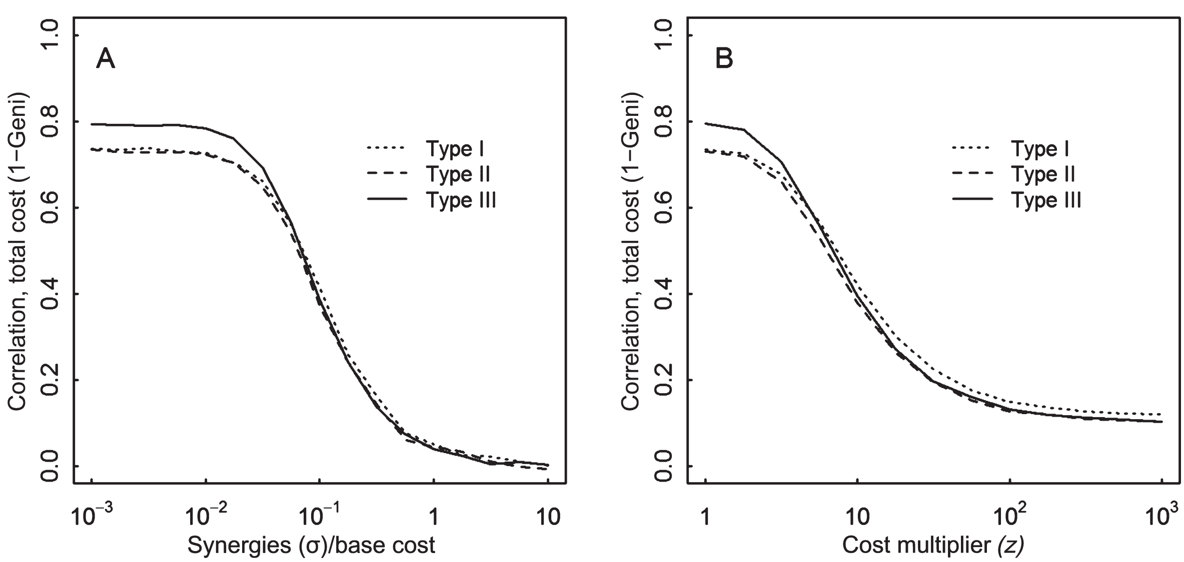


FIG. 3. Correlation between the cost of restoration and stressor heterogeneity (vertical axes) as a function of (A) the magnitude of the variance in interactions among stressors and (B) the magnitude of the variance in differences in the costs of remediating stressors in simulated multi-stressor landscapes.

affect the correlation between cost and stressor heterogeneity. When all stressors were described by equivalent cost functions ($z$ = 1), the total cost of restoring a site was highly correlated with stressor evenness (Fig. 3B; note this correlation was equivalent to that in Fig. 3A when synergies were small). As $z$ increased in magnitude, the correlation between total cost and stressor evenness declined, eventually approaching 0.1 when the most expensive stressor was about $10^3$ times more expensive to restore. Thus, stressor heterogeneity is a reliable metric of cost when stressors are all equivalently costly to restore, but an unreliable metric when one or more stressors are orders of magnitude more costly than others. In that case, the cost of restoring a site is determined primarily by the intensity of the most expensive stressor(s).

### *Heuristic translation of the model*

Inspired by our analytical and simulation results, we propose a simple rule of thumb for guiding restoration investments in multi-stressor landscapes: among sites with equivalent levels of cumulative stress, restoration investments should be targeted at sites with the highest stressor heterogeneity. The rationale for this heuristic is two-fold. First, parsimony dictates that the fewer stressors that must be addressed to achieve a desired improvement in ecosystem condition, the more cost-efficient restoration efforts will be, all else being equal. High stressor heterogeneity arises when some stressors have high intensity and others have low intensity, such that large reductions in cumulative stress can be achieved by focusing restoration on a relatively small number of high-intensity stressors. This is true regardless of whether remediation efforts reduce a particular stressor completely or partially; in both cases, cumulative stress can be alleviated most effectively by selecting sites where a modest number of serious stressors can be tackled and the remaining stressors are already at low levels. Our analytical and simulation results suggest that this logic of parsimony should apply to all sites except those dominated by strong positive interactions among stressors or sites dominated by stressors that are disproportionately costly to remediate.

The second rationale for this heuristic stems from the high degree of uncertainty surrounding stressor interactions. In multi-stressor landscapes, ecological restoration can have negative effects when the remediation of one stressor increases the severity or impact of another (i.e., antagonistic stressor interactions; Crain et al. 2008, Darling and Côté 2008, Brown et al. 2013), but these interactions are often complex and difficult to predict. Sites that require the fewest types of intervention have the lowest odds of unexpected antagonistic interactions. Accordingly, prioritizing sites with high stressor heterogeneity, where only a modest number of stressors must be addressed, represents a conservative or precautionary approach because it limits the chance that unexpected outcomes will jeopardize the success of restoration efforts.

## Case studies: Laurentian Great Lakes and global rivers

We propose using stressor evenness and cumulative stress as complementary indices that together provide information about the practical challenges of restoring a site to improved condition. To demonstrate this approach, we used data from recent multi-stressor mapping analyses of the world's rivers (Vörösmarty et al. 2010) and the Laurentian Great Lakes (Allan et al. 2013). In each case, our goal was to use stressor heterogeneity to identify sites at which the practical challenges of restoration are expected to be lowest (hereafter "restoration opportunities") and to demonstrate this approach across the entire cumulative stress spectrum, from relatively pristine sites to those that are highly degraded.

The Great Lakes dataset consists of raster data layers for 34 stressors and for CS across the entire basin, each at a 1 × 1 km resolution. Cumulative stress represents the summation of local stressor intensities weighted by an expert-derived index of the relative ecological impact of each stressor (Allan et al. 2013). The global rivers dataset consists of raster data layers for 23 stressors and for CS, each at a 0.5° (~50 × 50 km) resolution. CS was again based on an additive combination of stressor intensities and impact weights (Vörösmarty et al. 2010). Our process for identifying restoration opportunities from a set of individual stressor maps consists of three steps (illustrated in Fig. 4). First, we combined all individual stressor maps (Fig. 4A–D) into two intermediate map products: a map of cumulative stress (CS), calculated using expert-derived weightings as in the original papers (Fig 4E), and a map of stressor heterogeneity calculated using the Gini index (Fig. 4F). The Gini index is widely used in economics as a measure of inequality among elements in a set. In our stressor context, it takes values from zero (all stressors have identical intensity) to one (a single high-intensity stressor amidst many zero-intensity stressors). Preliminary analyses yielded similar patterns based on using the coefficient of variation as an index of heterogeneity (Appendix S2). Second, to compare sites of similar CS, we grouped sites into 100 bins representing 1% increments of CS. Third, within each CS bin, we selected the 10% of pixels with the greatest stressor heterogeneity, reflecting an arbitrary threshold identifying sites at which the practical challenges of restoration are most likely to be low (inset of Fig. 4). The set of sites identified as restoration opportunities was robust to alternative stressor normalization methods and measures of heterogeneity (see Appendix S2). For simplicity, we refer to each map pixel as a site, though we recognize that the relevant scales for stressor remediation vary and that multi-stressor datasets are best interpreted at broad spatial scales.

In the Great Lakes, the set of sites identified as restoration opportunities had broad geographic coverage

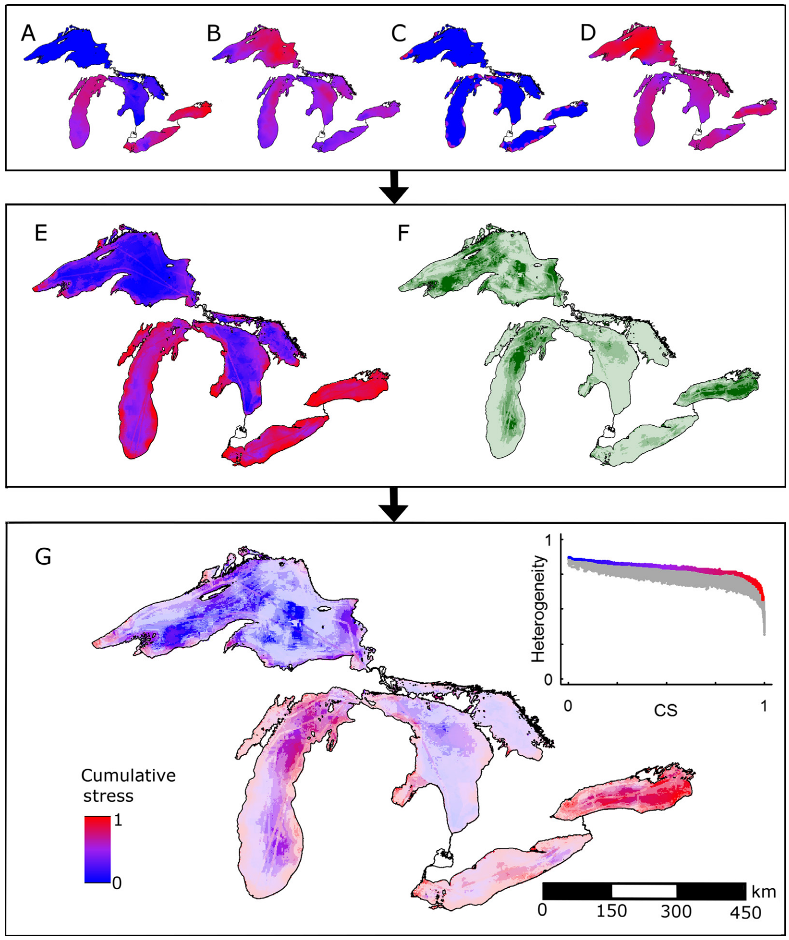


FIG. 4. The derivation of a map of restoration opportunities from a set of individual stressor maps. A set of individual stressor maps (A–D shows four of 34 maps used) are combined into (E) a map of cumulative stress and (F) a map of stressor heterogeneity, calculated using the Gini index. These two maps are then combined into (G) a single map of restoration opportunities by selecting the sites within the top decile of stressor heterogeneity for similar levels of cumulative stress (inset on G).

(Fig. 4G), highlighting opportunities for cost-effective restoration across the entire basin. Restoration opportunities exist in all five Great Lakes, but high opportunity sites were often spatially clustered and more prevalent in some regions than others. For example, Lakes Erie and Ontario have similar levels of cumulative stress, yet opportunities were more prevalent in Lake Ontario than in Lake Erie. Opportunities were equally prevalent in littoral (<5 m depth, or <3 m in Lake Erie; 12.66% of sites were high opportunity) and offshore waters (>30 m depth, or >15 m in Lake Erie; 11.33% of sites), but were less common in the sub-littoral zone (5–30 m depth, or 3–15 m in Lake Erie; 3.83% of sites). At the high cumulative stress end of the spectrum (0.9–1.0 CS), high stressor heterogeneity occurred primarily in the littoral zone, yet high heterogeneity and low cumulative stress (0–0.1 CS) were found exclusively offshore.

Several specific stressors were often the single most intensive stressor at high opportunity sites in the Great Lakes. Among all sites classified as restoration opportunities, non-native fish stocking was the most dominant stressor in 31.62% of sites, followed by copper contamination (28.10%), sea lampreys (12.42%), and PCBs (6.79%). Among sites with high stressor heterogeneity but low (0–0.1) CS, invasive mussels were the most dominant stressor in 39.22% of sites, followed by susceptibility to water level alteration (28.76%), non-native fish stocking (17.78%), and shipping (11.59%). Sites with high heterogeneity and also high (0.9–1.0) CS were dominated by a different set of stressors: copper contamination (59.21%), water warming (33.78%), and sea lampreys (13.03%).

The Great Lakes Restoration Initiative (GLRI) offers a unique opportunity to evaluate whether actual restoration sites would have been selected as opportunities under our approach. We calculated stressor heterogeneity within a 5-km buffer around the coordinates reported for each of the 277 projects funded between 2010 and 2012 (GLRI 2014). To our surprise, these major restoration investments have been disproportionately

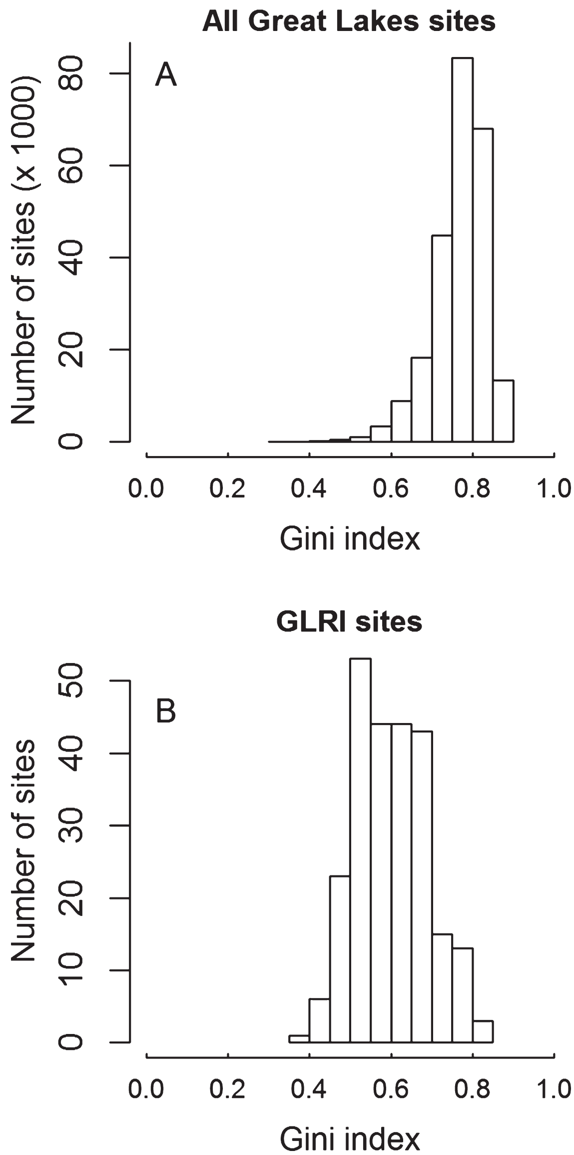


FIG. 5. Recent restoration investments in the Laurentian Great Lakes have been disproportionately targeted at locations with numerous problematic stressors. Histograms are of the Gini index (A) at all 241 943 pixels in the Great Lakes and (B) at 277 GLRI sites. Lower Gini scores indicate the presence of multiple high-intensity stressors.

targeted at locations where numerous problematic stressors give rise to high CS (Allan et al. 2013) but strikingly low heterogeneity (Fig. 5). Indeed, >75% of GLRI sites occur within the lowest decile of stressor heterogeneity, indicating that many different restoration actions would be needed to substantially improve ecosystem condition.

In the global rivers dataset, the set of sites identified as restoration opportunities also exhibited both broad geographic coverage and spatial clustering (Fig. 6). Opportunities exist on all continents, but exhibit spatial clustering such that there is much higher concentration of opportunities on some continents (e.g., North America) than others (e.g., South America). Sites with high stressor heterogeneity but low (0–0.1) CS were typically clustered in high northern latitudes. Conversely, sites with high heterogeneity and high (0.9–1.0) CS were globally distributed with particular concentrations in western and southern Africa, India, and China.

In the world's rivers, several specific stressors were often the single most dominant stressor in high opportunity sites. Among sites classified as restoration opportunities, non-native fishes were the most dominant stressor in 29.1% of sites, followed by fishing pressure (25.7%), mercury pollution (14.1%), and fragmentation (12.7%). Among sites with high stressor heterogeneity but low (0–0.1) CS, mercury was the most dominant stressor in 79.1% of sites, followed by aquaculture (11.7%) and fishing pressure (9.0%). Sites with high heterogeneity and also high (0.9–1.0) CS were dominated by non-native fishes (41.4% of sites), human water stress (18.5%), and river fragmentation (13.6%).

## DISCUSSION

Our prioritization framework is rooted in parsimony arguments for selecting restoration sites to maximize ecological return on investments in remediation. This approach leverages the increasing availability of spatial data on the severity of a wide variety of stressors (Danz et al. 2007, Halpern et al. 2008, Vörösmarty et al. 2010, Allan et al. 2013), which is generally analyzed solely from the standpoint of cumulative stress due to a lack of information on restoration costs or interactions among stressors (Crain et al. 2008, Darling and Côté 2008, Halpern and Fujita 2013). We find that the practical challenges of restoration will typically be negatively correlated with the evenness of stressor intensities at a site, suggesting that a simple index of stressor heterogeneity can be quite helpful for identifying opportunities to most improve ecosystem condition by remediating a modest number of stressors.

For most ecosystems, detailed data on restoration costs are unavailable (Bernhardt et al. 2007). Our analytical and simulation model results (Fig. 3A, B) constitute a sensitivity analysis that reveals that the stressor heterogeneity index is robust to considerable uncertainty in the details of the cost functions. We find that stressor heterogeneity will be strongly correlated with restoration cost except in three cases: when one or more dominant stressors are orders of magnitude more expensive to restore (per unit of stressor intensity) than other stressors, when synergies among stressors are so large that they are the primary determinant of the cost of restoring a site, and when sites are dominated by stressors that exhibit diseconomies of scale in restoration costs. If managers are able to avoid these three exceptional cases based on expert knowledge, then further detailed cost data are unlikely to be necessary in order to use stressor

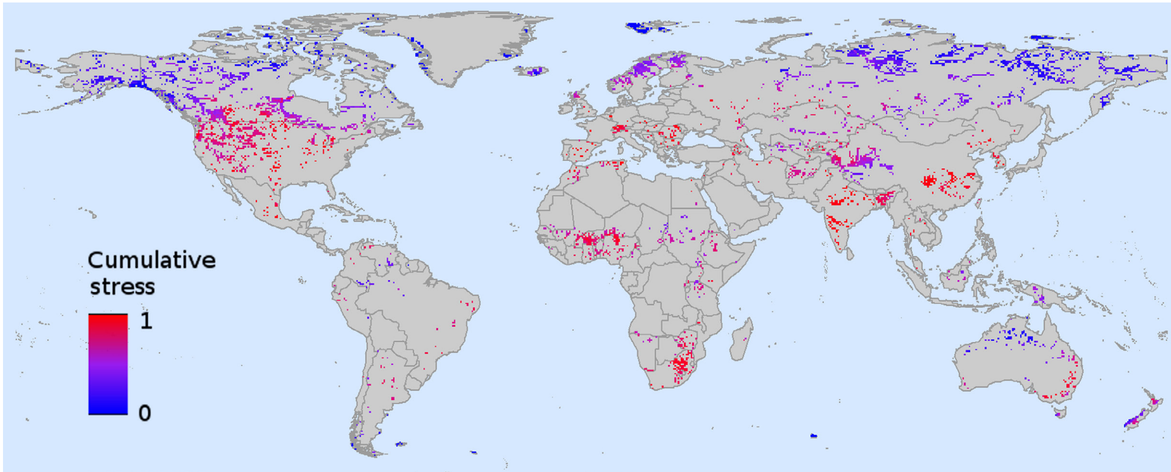


FIG. 6. Restoration opportunities in the world's rivers. High opportunity sites are those within the top decile of stressor heterogeneity among sites with comparable cumulative stress.

heterogeneity as a general metric to aid in identifying restoration opportunities.

We envision that the stressor heterogeneity metric will be most useful as a first-pass filter for rapidly reducing the number of candidate restoration sites, setting the stage for more formal prioritization methods. Restoration efforts that address one stressor in isolation may have little real benefit if they fail to account for the other problematic stressors at a site (Evans et al. 2011, Wilson et al. 2011, Brown et al. 2013), yet limited data on restoration costs and benefits typically precludes formal return on investment (ROI; Auerbach et al. 2014) or structured decision making (SDM; Tulloch et al. 2015) analyses that account for all problematic stressors in an ecosystem. By selecting sites with the highest stressor heterogeneity (e.g., our upper decile criterion), managers could quickly eliminate from consideration those sites with numerous problematic stressors. Importantly, because sites with high stressor heterogeneity have only a modest number of high-intensity stressors, they are well suited for further prioritization via ROI or SDM analyses that focus on that key subset of stressors.

Our framework for estimating restoration costs is equally applicable to any of the various motivations for restoring a site. Some organizations prefer to target restoration efforts toward high biodiversity sites, others target sites with important ecosystem services, and yet others choose sites based on an organizational mandate to remediate a particular class of stressors (Clewell and Aronson 2006, Bullock et al. 2011, Hallett et al. 2013). For each of these priorities, stressor heterogeneity can reveal sites at which restoration would have high benefit in return for addressing a minimal number of stressors. For example, intersecting maps of restoration opportunities with maps of ecosystem services (Turner et al. 2007, Naidoo 2008, Egoh et al. 2009, Nelson et al. 2009, Allan et al. 2013) would highlight locations where restoration efforts could best contribute to sustaining key services. Similarly, intersecting maps of restoration opportunities with maps of biodiversity or priority species (Auerbach et al. 2014) would highlight locations where mitigation of only a subset of stressors could substantially augment conservation efforts. Because our metric is applicable across broad spatial scales, it could also be used to support regional coordination of conservation investments, which can be up to 10 times as cost effective as local-scale planning (Kark et al. 2009, Mazor et al. 2013, Neeson et al. 2015).

Stressor heterogeneity is a particularly useful metric for agencies mandated to manage a particular class of stressors, because it can be used to identify sites where remediation of their focal stressor alone would result in a large decrease in cumulative stress. For example, 59% of the sites in the Great Lakes with high CS and high heterogeneity were impacted most strongly by copper in sediments. If environmental management agencies (e.g., USEPA or Environment Canada) focused their efforts on these sites, remediation of sediment metals alone would result in a relatively large decrease in cumulative stress. This example illustrates the potential for stressor heterogeneity to serve as a first-pass filter that drastically reduces the number of candidate restoration sites: by focusing further prioritization efforts exclusively on high heterogeneity sites, managers could more feasibly perform the detailed analysis needed to predict the probability of successful management (Bottrill et al. 2008, Joseph et al. 2009). In that context, it is particularly striking that the hundreds of Great Lakes sites selected for major restoration investments under GLRI show low stressor heterogeneity along with high CS (Fig. 5). This pattern signifies that remediation of one or a few stressors, as was typical in GLRI projects, would have limited scope for ecosystem response due to the continuing occurrence of other high-intensity stressors. While the

GLRI site selection process surely incorporated many practical and societal issues that are not considered here, our results suggest that accounting for stressor heterogeneity could have been helpful.

A key assumption of our approach is that all stressors are equally remediable. In reality, some stressors, such as those associated with climate change, cannot be remediated through local action. As a result, a site impacted primarily by climatic variables might exhibit high heterogeneity but offer few practical avenues for remediation. Thus, common-sense screening of both stressors and sites must be involved in applying cumulative stress or stressor heterogeneity metrics to restoration prioritization. Our approach is also constrained by the uncertainties and assumptions common to all threat mapping efforts (Halpern and Fujita 2013). However, threat mapping methods continue to be refined, and increasingly accurate threat maps are emerging for many of the world's ecosystems. Our framework provides a means to leverage these increasingly sophisticated spatial data sets to aid in the prioritization of restoration investments.

Our development of stressor heterogeneity as a metric of restoration feasibility has interesting parallels with the quantitative characterization of biodiversity. It has long been recognized that biodiversity at a site has two major dimensions: species richness and species evenness (Hayek and Buzas 1997). As a result, the diversity indices of choice integrate both richness and evenness (Magurran 2004). In contrast, multi-stressor analyses have focused purely on generating defensible indices of cumulative stress by carefully weighting stressors (Teck et al. 2010) or using factor analyses to distill stressor associations (Danz et al. 2007). This focus on CS alone results in discarding much of the information in multi-stressor datasets. Indeed, even a simple two-stressor case illustrates how stressor heterogeneity can be functionally independent of CS (Fig. 2). When comparing large numbers of sites for restoration purposes, our model results and case studies suggest that accounting for stressor evenness can substantially boost potential ecological return on restoration investments when multi-stressor data are available. Moreover, if additional considerations, such as ecosystem services or biodiversity, can be depicted spatially, analysis of stressor heterogeneity can be integrated with these other factors in a similar fashion to the example of CS offered in this paper. Ultimately, the more information that is incorporated into prioritization procedures, the higher return on restoration investments is likely to be for society.

High-resolution stressor mapping has become a key component of modern conservation science (Tulloch et al. 2015). By more fully utilizing the information within multi-stressor datasets, it may be possible to substantially reduce the cost of improving ecosystem condition through restoration efforts. Application of our stressor evenness heuristic to two prominent multi-stressor datasets suggests that restoration opportunities are geographically widespread, indicating potential for selecting portfolios of projects in which diverse constituencies have a stake. By design, this range of sites represents the full spectrum of conservation efforts, from preserving relatively pristine areas to remediating heavily degraded ones, thereby suiting the expertise and mandates of a wide range of organizations (Game et al. 2008, Ban et al. 2010). As multi-stressor datasets become increasingly available for the world's ecosystems, further strategic use of these data can provide an efficient means of prioritizing sites based on their potential for cost-effective restoration efforts.

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