

Examining sources of ecological resilience to climate change for restoration planning

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Abstract

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Restoration ecology is a burgeoning field and ecological restoration efforts are becoming more wide-spread. However studies reveal that many restoration efforts fail to accomplish their objectives because they do not address the root cause of degradation or because there is a mismatch between the scale of the problem and scale of the restoration action. Currently, practitioners are faced with the dual challenge to restore system functioning while preparing for unknown impacts from anthropogenic climate change. Climate change could serve as the needed catalyst to shift approaches that allow for natural variability and shifting dynamics to accommodate for unknown climate change impacts. Restoring natural sources of resilience is believed to be an effective way to build adaptive capacity to climate change. There are however many questions surrounding the pragmatic application of resilience theories. One such barrier is identifying what factors within a system influences response to disturbance. Consequently, a

critical first step is to identify the dynamic processes and associated attributes that influence resilience in natural systems. In this study, I examined published literature to identify a suite of ecological attributes that influence resilience, either through resisting change or recovering from disturbance. I then developed a Decision Support Tool (DST) to navigate the resilience attributes and to help integrate resilience planning and monitoring into restoration projects.

Key words: ecological restoration, ecological resilience, climate change, recovery, resistance, decision support tool

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1.0 INTRODUCTION

Substantial alterations in earths' ecosystems have caused many governmental agencies, non-profit organizations, and private interest groups to invest in restoration efforts. Environmental restoration has become a management priority often directed by powerful legal mandates such as the Endangered Species Act and the Clean Water Act. According to a 2005 synthesis of restoration projects in the U.S. (the National River Restoration Science Synthesis, NRRSS), over \$1 billion is spent each year on riverine restoration alone (Bernhardt et al. 2005). Restoration activities vary in scale and by objectives, ranging from small projects that focus on a single species to larger projects that seek to restore ecosystem functions. Yet despite monumental investment, ecological restoration has been unsuccessful in slowing declines in habitat quality and extinction rates (Beechie and Bolton 1999; Bernhardt et al. 2005; Palmer et al. 2005; Norton 2009; Rey Benayas et al. 2009). For example, a systematic review of 89 restoration assessments revealed a positive correlation between an increase in biodiversity and ecosystem service measures following restoration but in all cases those values remained lower in restored areas when compared to intact reference ecosystems (Rey Benayas et al. 2009). Many ecologists believe that restoration projects often fail to reach their goals because they do not focus on restoring (or monitoring) the processes that support the attributes one is trying to remediate (Simenstad et al. 2005; Herrick et al. 2006; Beechie et al. 2010). The necessity to shift our focus from restoring stable states to that of supporting dynamic processes is especially pertinent in the face of a changing climate (Choi et al. 2004; Palmer et al. 2005).

Anthropogenic climate change imposes multiple stressors on systems already under stress from human use, with consequences for restoration outcomes (Palmer et al. 2008). For example, rapid long-term changes in physical factors such as temperature and hydrology could undermine

the success of restoration projects. In this context, stream restoration planning using precipitation frequencies based on historical data will likely be inappropriate in some river basins and could influence site assessment and undermine project design. Consideration of climate change impacts will need to be integrated into restoration planning to create resilient systems capable of persisting under conditions of climate change.

What do concepts like resilience to disturbance mean in ecology and how do they differ from other concepts like integrity and complexity? While complexity does consider variability within a system, it overlooks the potential for dynamic transitions between alternative states and does not identify sources that maintain crucial ecosystem processes. Ecological integrity, or the ability of an ecosystem to support certain components and functional organization within their natural ranges of variation shares similarities with resilience. However whereas integrity focuses on the stability of a system, ecological resilience focuses on feedbacks, unpredictable change, and variation. As such, resilience theory can be applied to systems exposed to rapid climate change (Holling 1996; Parrish et al. 2003). While resilience theory as treated in the literature is fraught with inconsistencies and has proven difficult to measure (Thrush et al. 2009), it is recognized as an important concept, especially in relation to climate change perturbations. In this paper I use the resilience perspective of Walker et al. (2004), which is defined as the capacity of a system to absorb disturbance and reorganize in ways that retain essentially the same functions, structures, identities, and feedbacks. This definition includes notions of resistance to change and recovery from change, both of which are prominent in my treatment of the problem.

Several studies identify restoration as a crucial element for improving ecosystem resilience to climate triggered impacts (Hansen et al. 2003; Beatley 2009; Seavy et al. 2009; Beechie et al. 2012). Over time, human actions have caused a loss of resilience in some systems; that is, human

actions have reduced the ability of ecosystems to adapt to various impacts (Folke et al. 2004; Walker and Salt 2006). By restoring dynamic processes that promote natural variability and biodiversity, resilience within ecological systems can be fostered, ultimately minimizing the risk of dramatic ecosystem change, sharp declines in populations, and loss of ecosystem services (Folke et al. 2004; Beechie et al. 2010). Consequently, a first step in fostering resilience is to identify the dynamic processes within ecosystems that confer resilience. Currently there is limited knowledge of what dynamic processes or ecological attributes confer resilience and this gap creates a barrier to implementing resilience planning in ecological restoration.

Here I address the problem of climate impacts on restoration outcomes and identify a method to integrate resilience into project planning and monitoring. My primary research question is whether there are certain biophysical attributes that contribute disproportionately to resilience to climate change. I addressed this question by investigating treatments of ecological resilience within the peer-reviewed literature to create a list of empirically tested attributes that have been shown to confer resilience. I then designed a Decision Support Tool (DST) intended to help restoration practitioners select appropriate attributes suited to their management context and objectives. Identifying sources of ecological resilience is a critical step to develop the adaptive capacity of restoration projects and ultimately, the ecosystems we are trying to restore.

2.0 METHODS

2.1 Literature Selection and Review

I performed a literature review to evaluate ecological attributes and associated metrics that have been identified in the scientific literature as conferring resilience. Using the Web of Knowledge,

I searched on the following terms: (river* OR stream OR (wetland NOT in title) OR ecosystem OR environment*) AND (restor* OR recov* OR re-creat* OR rehabilitat*) AND (resilienc* OR “ecological integrity”). I restricted my search to papers published from 2009-2013. From a total of 915 search results, I selected 232 articles for further review if the title described a scientific study investigating the resilience of some ecological characteristic(s). Of the 232 articles, 111 were selected for full review based on relevance to the study objectives as inferred from the abstract. I gleaned 59 additional articles from literature cited in the 111 selected articles based on my best professional judgment of their fit with the goals of this study. These articles were added to the analysis for a total of 170 articles analyzed in this study (see Appendix).

2.2 Resilience Attribute Weighing

Each attribute was initially evaluated using the following criteria:

1. The attribute is general enough to be useful in a variety of ecosystems or for a variety of different species
2. The attribute is discrete from other attributes and is measurable
3. The attribute is characteristic of an ecological system

I created a database in which every attribute was recorded verbatim from the article and included associated information regarding the source of the publication, the ecosystem context, metric(s) used to measure or monitor the attribute, and whether the attribute was identified as conferring resistance to or recovery from disturbance. This process produced 140 resilience metrics. I then grouped the attributes into major categories and combined attributes that were similar to produce a list of 51 resilience attributes classified in five major categories (Table 1).

2.3 Climate Change Filter

I then subjected the 51 attributes to a climate filter to identify which attributes directly interact with climate change variables. An attribute passed through the climate change filter if it was discussed in relation to climate change or impacts directly associated with climate change (e.g., temperature increase, flood, drought, etc.). A total of 45 attributes remained after the climate filter was applied.

2.4 Decision Support Tool

To help navigate the list of 45 resilience attributes for restoration efforts, I created a DST to assist practitioners in selecting a subset of attributes more appropriate for their restoration plans or specific projects. Resilience attributes that passed through the climate filter were classified according to two criteria and a filter tool was applied in order to allow practitioners to select a set of resilience attributes that were best suited for the context and focal scale of their particular project (Table 2).

2.4.1 Attribute Classification

For the ‘ecological context of management project’ column, each attribute was classified according to what type of project it is best suited for (e.g., species-specific project, habitat-specific project, or system-wide project). For example, the population size attribute was classified as species because this attribute would be of most interest to a project focused on species restoration as opposed to a habitat or system focused restoration project. A number of

attributes were relevant to more than one project type and therefore were assigned more than one category.

For the ‘focal scale’ column, I classified each attribute according to what scale of focus it is best suited for (individual, population, site, or system). For example, the refugia or support areas attribute was classified as site and ecosystem because these attributes would typically be measured at these scales of focus. Several attributes can have more than one focal scale and were categorized appropriately. I attempted to classify each attribute based on a diversity of different project types. Some users may need to tune some classifications to meet the needs of particular systems or projects.

Table 2: Attributes classified according to the methods described above.

	Resilience Attributes	Example Metrics	Ecological Context of Management Project			Focal Scale (individual, population, site, ecosystem)
			Species	Habitat	System	
Individual Attributes	Individual growth rate	time to reach reproductive maturity	x			individual
	Individual size	large bodied, small bodied	x			individual
	Life span		x			individual
	Individual characteristics that favor flexibility or adaptability *	recruitment potential, generation times, fecundity, dispersal ability	x			individual
	Reproductive strategy	rapid, brooding, times/yr	x			individual
	Adaptation to disturbance *	biomass, survival, dormancy, foraging habit	x			individual
	Presence of propagules	recruitment, ramet survivorship	x	x		site
	Dispersal potential *	rates, distance, mode	x	x		individual
	Efficient water capture and use	depth of root growth	x			individual, site
Population Attributes	Genetic diversity *	quantity of genetic variation	x			population
	Population size *	small, large	x			population
	Population density *	biomass %, LAI, cover	x	x		population
	Population growth rate		x			population
	Population age structure	mix of successional stages, older, younger	x			population
	Connectivity between populations*	movement of propagules, use by large	x			population, ecosystem
Community Attributes	Community structure	rugosity, stable root structures, % cover		x	x	site
	Species assemblage *	total # of taxa, dominance of tolerant		x	x	site
	Species (alpha) diversity *	# of species, # meanders, DO concentrations		x		site
	Functional diversity *	subordinate plant species, reaction to		x	x	site, ecosystem
	Response diversity			x	x	site, ecosystem
	Functional redundancy *			x	x	site, ecosystem
	Connectivity among communities	distance from other existing habitat (scaled to daily home ranges)		x	x	ecosystem
Ecosystem Attributes	Habitat area	Km radius, stream size	x	x	x	site, ecosystem
	Habitat structure	structural complexity, topography, bathymetry, edginess	x	x	x	site
	Habitat condition *	presence of vegetation, soil health, H2O quality, type of human development	x	x	x	site, ecosystem
	Temporal variability in habitats *	hydrologic, thermal, water column mixing			x	ecosystem
	Spatial variability in habitats *	juxtaposed habitats, thermal, hydrologic	x	x	x	ecosystem
	Refugia or support areas *	riparian buffer width, mesohabitats	x	x		site, ecosystem
	Connectivity between different habitats *	corridors, fragmentation, energy flows	x		x	ecosystem
Process Attributes	Connectivity to refugia areas	presence of backwater areas, hyporheic zone	x		x	ecosystem
	Energy flows *	high flushing rate, nutrient cycling, food			x	site, ecosystem
	Natural release from competition or predation	number of herbivorous fish	x			population
	Sedimentation	accretion rate	x	x	x	site, ecosystem
	Soil and air carbon balance	available soil C		x		site
	Hyporheic flows	presence of	x	x	x	site, ecosystem
	Flow regime	timing, flow intensity	x		x	site, ecosystem
	Groundwater contributions	presence of	x	x	x	site, ecosystem
	Structural legacies *	belowground structure, percentage cover	x	x		site
	Water infiltration	soil moisture content, run-off velocity		x		site
	Feedbacks between physical and biological	veg. growth & sedimentation			x	site, population, ecosystem
	Recovery (time) after disturbance	to a certain size, biomass	x	x		species, site
	Natural disturbance history *	heterogeneity of habitat types	x	x	x	site, ecosystem
	Random environmental variability	flood events, vegetation patterns	x	x	x	site, ecosystem
	Disturbance duration and intensity	pulse, press, magnitude, spatial or temporal	x	x	x	site
Degree of exposure to human pressures	pollution levels, overfishing, water withdrawal	x	x	x	site, ecosystem	

*Attributes cited 8+ times in literature

2.4.2 Attribute Selection

Using the DST, the practitioner selected the corresponding ecological context of their management project (species-specific, habitat-specific, or system-wide). The same procedure was done for the focal scale column where the practitioner asked, what type of metrics are most useful for their given project context (individual, population, site, or ecosystem). The focal scales for a species context project are typically the individual, population, or site whereas the focal scales for habitat or system based projects would be site and ecosystem. The output is a sub-set of resilience attributes more pertinent to the specific plan or project.

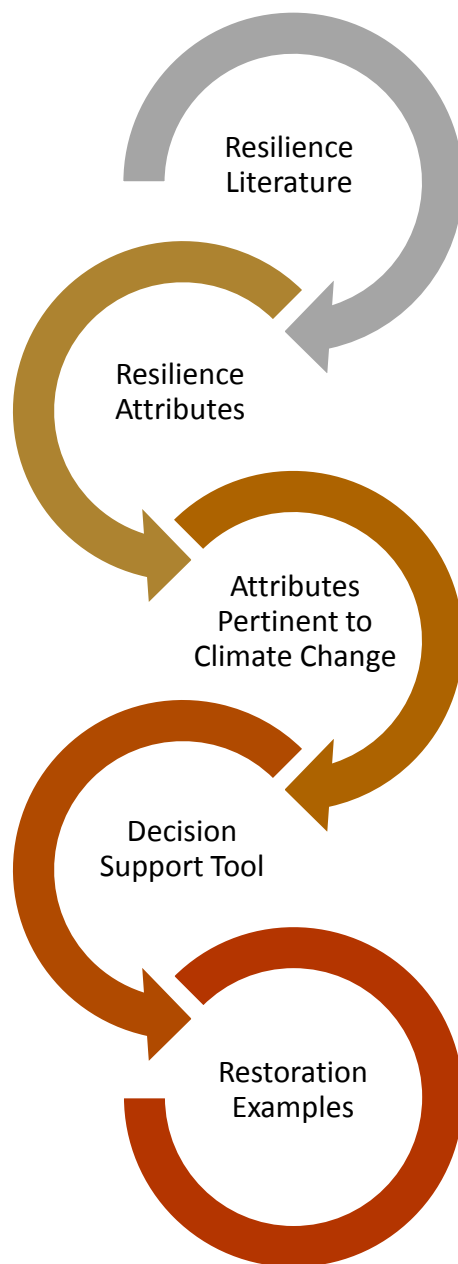
A project may contain elements that vary in ecological context and operate at more than one focal scale. Practitioners can either select the primary ecological context of their project or if there is more than one context they can explore multiple outcomes using the DST. The examples within this study (Tables 3, 4, & 5) were selected using a filter function in Microsoft Excel. This framework was intended to be flexible to serve a variety of different project types in any geographic region.

2.4.3 Sample Applications

Three sample applications of the DST are presented in section 3.4 using the methods described above (Tables 3, 4, & 5). Three different project types at different focal scales were selected to demonstrate how the DST functions and to highlight how attributes selected will differ according to the type of project. Examples include restoration of the Kissimmee watershed system at the ecosystem focal scale, restoration of a salmon population at the population focal scale, and restoration of vulnerable coral species at the site focal scale. The purpose was to demonstrate

how practitioners can use the tool to select appropriate resilience attributes to integrate into their projects. Using this tool is one way that resilience planning can be integrated into restoration efforts.

2.5 Project Conceptual Model



3.0 RESULTS

3.1 Literature Review

I limited my web-based search to papers published between 2009 and 2013. About 20 additional sources (12%) were included as relevant sources cited within papers from the original search.

The distribution across years of publications reviewed is shown in Figure 2. The distribution across systems is shown in Figure 3.

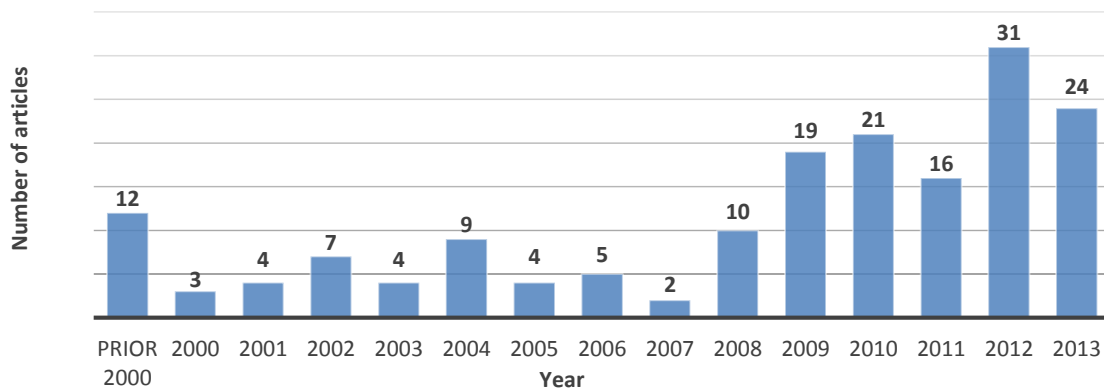


Figure 2: Frequency distribution of articles by publication year. A total of 170 sources were used in this literature review.

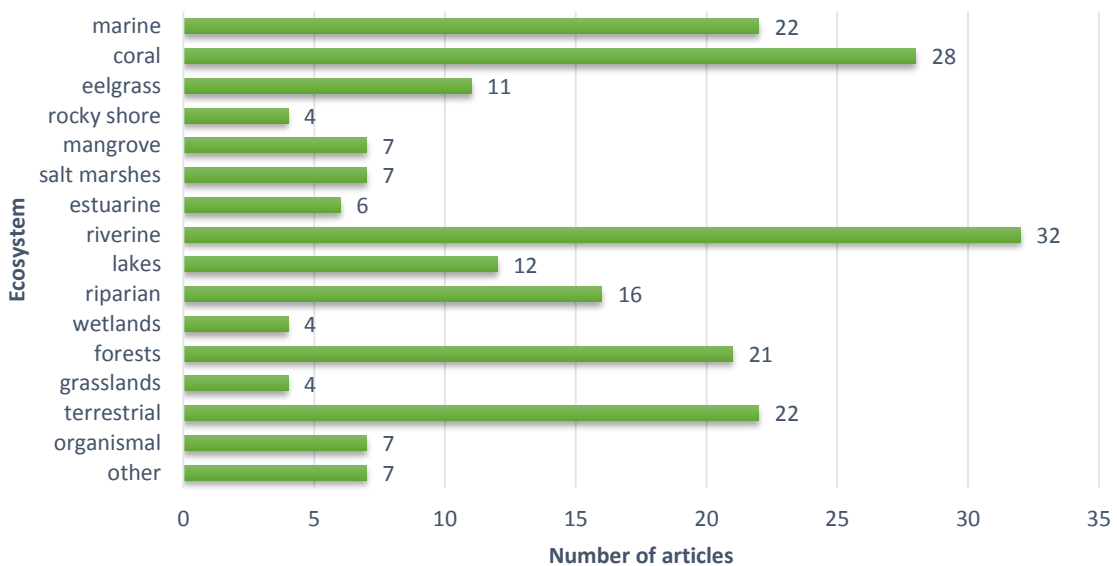


Figure 3: Frequency distribution of articles by ecosystem.

It is important to understand how the term resilience is interpreted in the literature. My research confirmed that the term is encumbered with inconsistencies throughout the ecological literature. Resilience was commonly used synonymously with recovery. Several sources for example referred to ‘the resistance and resilience’ of a particular ecosystem component. There was however a considerable body of literature identifying sources of resilience that resist perturbation (Table 1). A few sources considered resilience to comprise of the two key components I used in this paper (derived from McClanahan et al. 2012): that of resistance, or the ability of an ecosystem or community to persist through a disturbance and recovery, or the rate at which a system or community returns to its functional state (Pimm 1984; West and Salm 2003; Wang and Blackmore 2009; Downing and Leibold 2010; Proença et al. 2010; Brewer 2011; McClanahan et al. 2012).

3.2 Resilience Attributes

Attributes were classified into five categories that roughly equate to scale: 1) Individual Attributes, 2) Population Attributes, 3) Community Attributes, 4) Ecosystem Attributes, and 5) Process Attributes. The number of attributes varied across categories. Process attributes accounted for the largest number of attributes, while population attributes accounted for the fewest (Figure 4).

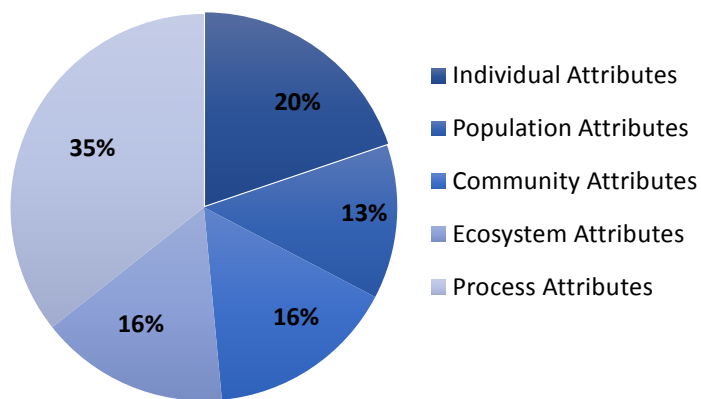


Figure 4: Percentage of Attributes by Category.

The number of citations varied by category (Figure 5). Process attributes accounted for the largest number of citations, and community attributes accounted for the fewest. Interestingly, the number of citations for biotic attributes (including the individual, population and community categories) was comparable to abiotic attributes (the ecosystem and process categories).

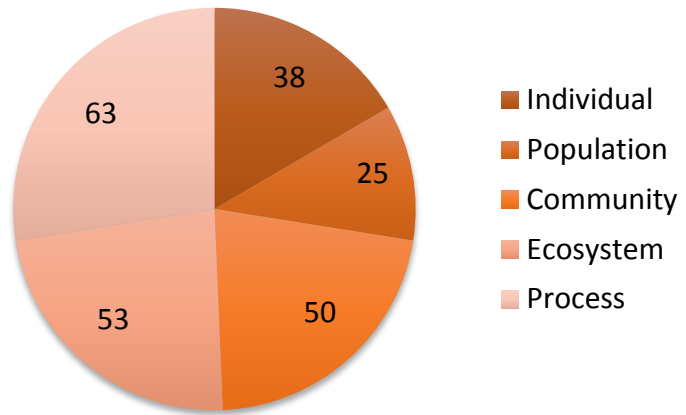


Figure 5: Number of Citations by Category.

Most attributes were identified in more than one article. Frequency of citation can be interpreted as a coarse measure of importance. The most frequently cited attributes were within the ecosystem category. While the process category accounted for the largest number of attributes and citations, each attribute tended to be cited less frequently than attributes in other categories (Table 1). The most frequently cited attribute in the process category was natural disturbance history. In the ecosystem category, connectivity between different habitats and spatial variability in habitats accounted for the greatest number of citations. Alpha diversity was cited most frequently in the community category and within the population category, population density and genetic diversity were the most frequently cited attributes. The attributes with the most citations within the individual category were the ability of organisms to adapt to disturbance, and individual characteristics that favor flexibility or adaptability.

Table 1: Resilience attributes identified in this literature review are first classified by physical and biological attributes. The attributes are then grouped into five major categories (Individual, Population, Community, Ecosystem, and Process). Also included is whether the attribute was identified as resisting or recovering from disturbance, and the number of times an attribute was identified by a different source. Attributes highlighted in grey did not pass through the climate filter.

Resilience Attribute Category		Grouped Attributes	Resistant	Recovers	Times Cited
Biological Attributes	Individual Attributes	(Biological) adaptation to disturbance	X	X	14
		Individual characteristics that favor flexibility		X	10
		Dispersal potential	X	X	10
		Individual size	X	X	7
		Presence of propagules		X	5
		Individual growth rate		X	4
		Life span	X	X	4
		Reproductive strategy	X	X	4
		Efficient water capture and use	X		2
	Population Attributes	Genetic diversity	X	X	9
		Population size	X	X	8
		Population density	X	X	10
		Population growth rate		X	1
		Population age structure	X	X	4
		Population (beta) diversity	X		2
	Community Attributes	Community structure	X	X	4
		Species assemblage	X	X	12
		Species (alpha) diversity	X	X	17
		Functional diversity	X	X	10
		Response diversity	X	X	7
		Functional redundancy	X	X	8
	Gamma diversity	X	X	2	
Physical Attributes	Ecosystem Attributes	Habitat area	X	X	6
		Habitat structure	X	X	6
		Habitat condition	X	X	14
		Temporal variability in habitats	X	X	10
		Spatial variability in habitats	X	X	20
		Refugia or support areas	X	X	13
		Connectivity between different habitats	X	X	18
		Food web complexity	X		2
		Large woody debris (LWD)	X	X	1
		Salinity		X	1
		Process Attributes	Connectivity to refugia areas		X
	Energy flows		X	X	12
	Natural release from competition or predation		X	X	3
	Sedimentation		X	X	4
	Soil and air carbon balance			X	2
	Hyporheic flows		X		2
	Flow regime		X	X	4
	Groundwater contributions		X		2
	Structural legacies			X	9
	Water infiltration		X	X	3
Feedback between physical and biological processes	X	X	2		
Recovery (time) after disturbance		X	5		
Natural disturbance history	X	X	16		
Random environmental variability	X	X	6		
Disturbance duration and intensity		X	12		
Degree of exposure to Human Pressures		X	5		

3.3 Climate Filter

A majority of resilience attributes (45 of the 51) were discussed in relation to climate change impacts or impacts directly associated with climate change. In Table 1, the shaded rows show the attributes that did not pass through the climate filter. These included population (beta) diversity, gamma diversity, food-web complexity, Large Woody Debris, salinity, and historical flow-disturbance regimes. It is important to acknowledge that the attributes eliminated in the climate filter process may confer resilience to climate change impacts in some situations, but such linkage was not apparent in the articles evaluated.

3.4 Sample Applications

The sample applications offered are examples of how the DST can be used to derive a sub-set of resilience attributes (Tables 3, 4, & 5). Selecting different project types demonstrates how a sub-set will differ depending on project context and focal scale. While not all the attributes may be useful for each restoration effort highlighted, this demonstrates a useful first step in identifying resilient attributes that could function at the appropriate context and scale of the selected project.

Example 1- Kissimmee River System: This example highlights how the DST will perform when a restoration plan or project is focused on restoring larger system processes such as restoration efforts to restore the Kissimmee River System in Florida. This restoration effort aims to reverse channelization and draining of wetlands to restore floodplain connectivity and restore ecosystem processes important to both the Kissimmee River and the Everglades ecosystem downstream.

The attribute categories present are community, ecosystem, and process (Table 3). The key resilience attributes within the community category are diversity and redundancy. Within the ecosystem category, habitat characteristics such as area, condition, and variability are present. These tend to be attributes that might support diversity or redundancy. The remaining attributes in the process category tend to be features that might drive habitat condition and therefore support the community attributes. Attributes related to connectivity appear in all three of the major categories.

	Resilience Attributes	Ecological Context of Management Project what is the context of your project?	Focal Scale what type of metrics are most useful given the project context?
Community Attributes	Functional diversity *	habitat, system	site, ecosystem
	Response diversity	habitat, system	site, ecosystem
	Functional redundancy *	habitat, system	site, ecosystem
	Connectivity among communities	habitat, system	ecosystem
Ecosystem Attributes	Habitat area	species, habitat, system	site, ecosystem
	Habitat condition *	species, habitat, system	site, ecosystem
	Temporal variability in habitats *	system	ecosystem
	Spatial variability in habitats *	species, habitat, system	ecosystem
	Connectivity between different habitats *	species, system	ecosystem
Process Attributes	Connectivity to refugia areas	species, system	ecosystem
	Energy flows *	system	site, ecosystem
	Sedimentation	species, habitat, system	site, ecosystem
	Hyporheic flows	species, habitat, system	site, ecosystem
	Flow regime	species, system	site, ecosystem
	Groundwater contributions	species, habitat, system	site, ecosystem
	Feedbacks between physical and biological processes	system	site, population, ecosystem
	Natural disturbance history *	species, habitat, system	site, ecosystem
	Random environmental variability	species, habitat, system	site, ecosystem
	Degree of exposure to human pressures	species, habitat, system	site, ecosystem

Table 3: Sub-set of resilience attributes for restoration focused on the system wide context at the ecosystem focal scale.

Example 2 - Restoration of a Salmon Population: This example demonstrates the outcome of the DST for a common restoration goal, which is to restore populations of a threatened or endangered species. In this example, I focus on restoring salmon populations in the western United States, which must achieve several important targets including adequate population size,

recruitment rates, spatial distribution, and diversity to be removed from the Endangered Species list. Recovery targets are established for each population within an Evolutionarily Significant Unit (ESU), and delisting criteria also consider whether habitat factors contributing to listing have been abated.

The categories present after running the selection criteria include only population and process attributes (Table 4). Characteristics pertinent to measurement of populations, such as population size, density, and age structure are dominant in the population category. In addition, genetic diversity and connectivity are key resilience attributes that may be useful for monitoring future performance in these populations. The attribute best suited for this type of project within the process category is release from competition or predation which in turn could affect several of the attributes within the population category.

Resilience Attributes		Ecological Context of Management Project what is the context of your project? <input type="text"/>	Focal Scale what type of metrics are most useful given the project context? <input type="text"/>
Population Attributes	Genetic diversity *	species	population
	Population size *	species	population
	Population density *	species, habitat	population
	Population growth rate	species	population
	Population age structure	species	population
	Connectivity between populations*	species	population, ecosystem
Process Attributes	Natural release from competition or predation	species	population

Table 4: Sub-set of resilience attributes for restoration focused on the species context at the population focal scale.

Example 3 - Coral Species Restoration: In this example I highlight another common approach in restoration, which is to restore a species at a particular site. This type of restoration goal is more common for sessile species and focuses either on restoring habitat for a species or ‘seeding’ a species to initiate recovery at a site.

Individual, ecosystem, and process categories are represented in the output of the DST (Table 5). The individual attributes speak to a species' ability to persist in an area. The ecosystem attributes are focused on habitat characteristics that may affect a species such as its condition, structure, or whether there are support areas present. The key process attributes may affect the habitat or species presence within a habitat for example structural legacies, disturbance, or degree of exposure to human pressures.

Resilience Attributes		Ecological Context of Management Project what is the context of your project? <input type="checkbox"/>	Focal Scale what type of metrics are most useful given the project context? <input type="checkbox"/>
Individual Attributes	Presence of propagules	species, habitat	site
	Efficient water capture and use	species	individual, site
Ecosystem Attributes	Habitat area	species, habitat, system	site, ecosystem
	Habitat structure	species, habitat, system	site
	Habitat condition *	species, habitat, system	site, ecosystem
	Refugia or support areas *	species, habitat	site, ecosystem
Process Attributes	Sedimentation	species, habitat, system	site, ecosystem
	Hyporheic flows	species, habitat, system	site, ecosystem
	Flow regime	species, system	site, ecosystem
	Groundwater contributions	species, habitat, system	site, ecosystem
	Structural legacies *	species, habitat	site
	Recovery (time) after disturbance	species, habitat	species, site
	Natural disturbance history *	species, habitat, system	site, ecosystem
	Random environmental variability	species, habitat, system	site, ecosystem
	Disturbance duration and intensity	species, habitat, system	site
Degree of exposure to human pressures	species, habitat, system	site, ecosystem	

Table 5: Sub-set of resilience attributes for restoration focused on the species context at the site focal scale.

4.0 DISCUSSION

4.1 Resilience Attributes

My results reveal that a considerable number of ecological resilience attributes have been identified in the literature. Several studies in recent years have focused on identifying sources of resilience throughout various ecosystems (Côté and Darling 2010; Maynard et al. 2010; Beechie et al. 2012; McClanahan et al. 2012; Thom et al. 2012; Bernhardt and Leslie 2013; Stromberg et

al. 2013). Maynard et al. (2010) used a literature review to distill a list of ‘resilience indicators’ that ‘conferred more resilience’. The authors then created an assessment framework using the resilience indicators and a focus group conducted the assessment and assigned resilience scores for a number of sites. In another study by McClanahan et al. (2012), a group of 50 scientists ranked and scored an existing list of ‘resilience factors’. Both studies assessed a list of ecological attributes that conferred resilience based on expert opinion within coral reef systems. Bernhardt and Leslie (2013) recently conducted a comprehensive study exploring sources of resilience to climate change within coastal marine ecosystems. From this review, three broad ecological mechanisms that underlie resilience were extracted: diversity, connectivity, and adaptive capacity.

This study differs from the foregoing in that I compiled resilience attributes from across many ecosystem types. I recognize that while not all attributes will be useful in every ecosystem, there is utility in consulting findings from similar and in some cases contrasting environments to accurately describe and quantify ecological resilience.

Certain ecological themes are more widely cited in the literature as conferring resilience. These themes include diversity, adaptability and connectivity, as highlighted in Bernhardt and Leslie (2013) but in addition, I identified habitat variability, natural disturbance history, habitat condition and presence of refugia or support areas as important attributes for ecological resilience. To follow I discuss some of these major themes and the dominant questions surrounding their application to resilience theory.

4.1.1 Biodiversity and the Insurance Hypothesis

The most frequently cited diversity attributes were alpha diversity, genetic diversity, and functional diversity. Duffy (2009) found that on average greater species richness increased resource use within trophic levels and accumulation of biomass and that the variance in these responses was reduced over time. Moreover, diverse communities have a higher chance of including either disturbance resistant species or species that are able to recover quickly from a variety of perturbations (Bernhardt and Leslie 2013; Mariotte et al. 2013). Ecosystems or communities with greater functional and response diversity are able to maintain important ecosystem processes that sustain function and result in ‘no net loss’ in productivity, often referred to as the insurance hypothesis (McNaughton 1977; Naeem and Li 1997; D’Odorico and Bhattachan 2012; Mijatović et al. 2013). Genetic diversity can provide this benefit by increasing the critical response diversity among populations and can help maintain ecosystem function (Ehlers et al. 2008; Bernhardt and Leslie 2013). Additionally, increased genetic diversity has been shown to promote population growth and improve fitness (Williams 2001).

There is still debate over the association between biodiversity and its influence on resilience. Not all findings support the insurance hypothesis. For example, Lanta et al. (2012) found that species richness and functional diversity were less resistant against drought stressed conditions than less diverse species assemblages in a greenhouse experiment. Outdoor experiments in the same study found no effect of diversity on community resistance. Similarly, in a study examining species richness in aquatic food webs, Downing and Leibold (2010) found that while respiration rates showed higher resilience in species-rich communities, they did not exhibit increased resistance to disturbance. In contrast, however, a number of studies have found strong causal links between diversity measurements and productivity or stability in a number of terrestrial and

aquatic systems (Duffy 2009), including seagrass (Stachowicz et al. 2008; Hughes and Stachowicz 2011), and forests (Virah-Sawmy et al. 2009a; Royer-Tardif et al. 2010).

4.1.2 Habitats

Biodiversity was identified as a dominant mechanism contributing to ecosystem resilience, and by extension, habitat conditions that influence biodiversity also function as important resilience attributes. Spatial and temporal variability in habitats has been observed to maintain higher levels of biodiversity (D’Odorico and Bhattachan 2013). A study conducted by Oliver and others (2013) found landscape structure, including increased heterogeneity within habitat patches, to influence resilience of populations to extreme climatic events. A landscape with a more heterogeneous habitat structure was more likely to contain refuge microclimates to aid in survival of the ringlet butterfly and a greater heterogeneity in habitat patches increased the likelihood of harboring species more resilient to extreme events (Oliver et al. 2013). Within river systems, spatiotemporal variability in flow and temperature regimes regulates suitable habitat and maintains flexible species adaptations (Caissie 2006; Chu et al. 2008; Stromberg et al. 2012). Milner et al. (2012) summarized that maintaining habitat heterogeneity can maximize resilience of aquatic species to altered flow regimes associated with climate change. While habitat variability functions as a driver for diversity at various scales, it has also been supported independently as a useful “measure of resilience to impending climate change” (Cowling and Pressey 2001).

Within the ecosystem category, certain attributes were identified as more important to ecosystem resilience. Among the most cited factors were habitat condition and a presence of refugia or support areas. Habitat condition is a description that broadly encompasses habitat

quality, which varied depending on the system in study. Within freshwater and salt marsh ecosystems, presence and type of riparian vegetation was found to create certain micro-habitats that promoted community resistance to dry conditions (Sridhar et al. 2004; D'Alpaos 2011; Stubbington and Datry 2013). Various soil health metrics were identified as crucial for aiding in recovery of forest ecosystems (Banning and Murphy 2008; Proença et al. 2010) and improving functional resilience in other terrestrial ecosystems (Griffiths et al. 2008; Vries et al. 2012; Zhang et al. 2013). Studies within coral reef systems identified water quality to be an important control of macroalgal growth, which can cause severe impacts to coral recruitment and overall reef resilience (Hughes et al. 2003; Adger et al. 2005; Olds et al. 2012). I also noted presence of refugia or support areas to be a prominent characteristic within habitats that support resistance and recovery of species (Yount and Niemi 1990; Nyström and Folke 2001; Caissie 2006; Millar et al 2007; Baker et al. 2008; Chu et al. 2008; Seavy et al. 2009; Kroon and Ludwig 2010; Chester and Robson 2011; Clark and Kershner 2011; Garcia et al. 2012; Milner et al. 2012; Stubbington 2012). These particular habitat attributes may not always influence resilience within each ecosystem but my findings suggest that identifying principal habitat characteristics may be an important consideration in monitoring resilience within an ecosystem.

4.1.3 Natural Disturbance History and Coupled Findings

A history of natural environmental fluctuations and disturbance is one process that maintains habitat heterogeneity and the variability induced by disturbances favors biodiversity (D'Odorico and Bhattachan 2013). Specifically, disturbance can regulate habitat structure at multiple scales which has the potential to affect species richness many years into the future (Poff 2002; Morimoto et al. 2013). A significant proportion of the literature identified presence of natural

disturbance as an important determinant for recovery rates, creation of alternate trajectories, and building biological capacity to adapt to or resist change. Systems that are naturally subjected to a variety of disturbances contain biota that have evolved life history traits that favor adaptability or flexibility (Yount and Niemi 1990; Li et al. 2012; Robinson 2012). Li et al. (2013) determined that bacterioplankton community compositions had developed a number of life history attributes that favored adaptation, such as high growth rates and phenotypic flexibility that explained their high resilience to the natural pulses of *Microcystis* blooms in a lake ecosystem. Within marine ecosystems, Neubauer et al. (2013) confirmed that a history of moderate exploitation within fisheries populations can increase their rate of recovery.

Disturbance plays an integral role in influencing biophysical characteristics and as such, certain ecosystems with a presence of natural disturbances were characterized as resilient (Poff 2002; Palmer et al. 2008; Seavy et al. 2009; White and Stromberg 2011; Frazier et al. 2013). In addition to presence, the magnitude and duration of a disturbance proved to be an important attribute conferring resilience within a number of different systems (Niemi et al. 1990; Yount and Niemi 1990; Bêche et al. 2009; Jacquet and Prodon 2009; Proença et al. 2010; Schaffner 2010; Speed et al. 2010; Graham et al 2011; Hughes and Stachowicz 2011; Lin et al. 2011; Sahib et al. 2011; Altieri et al. 2013; Leigh 2013). The effects of increased disturbances due to climate change however, do pose serious unknowns for resilience in these same systems. For example, holm oak woodlands are historically highly resilient to ~ 50 year intervals if fire frequency but if this rate increases as a response to climate change, the system may not exhibit the same degree of resilience. In a study examining resilience of fishes and invertebrates in streams to prolonged drought, Bêche and others (2009) found both severity and duration of drought disturbance to effect abundance and richness as well as general recovery of aquatic communities.

While I identified presence of natural disturbance history to confer resilience in several sources, it was often linked with other resilience attributes. As highlighted above habitat heterogeneity, adaptation to disturbance, life history traits that favor flexibility, and species richness are all resilience attributes that can be effected by natural disturbance. A number of attributes besides disturbance history functioned as drivers for other resilience attributes. For example a diverse flow regime that helps create spatial and temporal variability in physical habitat conditions (Poff 2002; Lobón-Cerviá 2009; Arthington et al. 2010; Kroon and Ludwig 2010). Habitat variability could therefore function as a resilience metric for flow regime. As previously discussed, habitat variability has been identified as a driver that enhances biodiversity. I presented these attributes separately however, in order to create a list that can better accommodate resilience studies in a number of different ecosystems.

4.1.5 Contradictory Findings

Conversely, some incongruous findings materialized in literature concerning the degree of exposure of an ecosystem or ecosystem component to human pressures. A number of studies identified either isolation from human pressures or less exposure to anthropogenic stressors to confer more resilience within their systems (McClanahan et al. 2002; Donohue et al. 2010; Gilmour et al. 2013). However in a recent study conducted over a wide geographic range of coral assemblages, Côté and Darling (2010) found that if there is a positive co-tolerance between non-climatic disturbance and climatic impacts among coral species, then some degree of degradation may, “increase the abundance of disturbance-tolerant species within a community and thus the ability of an ecosystem to resist the impacts of climatic disturbance”. The distinctions amongst these studies can be elucidative as more research is conducted in the future.

4.1.6 Cumulative Effects and Resilience

A number of resilience attributes I identified including exposure to human pressures, were often discussed in context of cumulative impacts. This is an important consideration when measuring resilience in a location subject to numerous human stressors in addition to a changing climate. In the literature a topic of major concern is the ability of ecosystems and their components to maintain resilience in the face of climate change among systems already under stress from cumulative human generated impacts (Palmer et al. 2005; Eklöf et al. 2009; Côté and Darling 2010). Multiple disturbance types can confound efforts to measure and monitor resilience within a system. It is beneficial to understand what something is resilient to and the presence of multiple stressors can make the answer more opaque.

4.2 Resilient Restoration

The DST was created to assist restoration practitioners to find appropriate attributes to measure and monitor for resilience within particular systems. I chose the ecological context of a management project to serve as the basis for categorizing the resilience attributes because the overarching goal or motivation will dictate other components of a project, such as objective setting and monitoring. The resilience attributes were selected based solely on existing literature. Outcomes will be context-dependent; these attributes will not work in all systems and some may prove to not be informative in certain systems. The attributes and their associated metrics should be a part of an adaptive management framework and evaluated for their usefulness in conferring resilience for specific projects. With increasing monitoring and measurement a more robust list of resilience attributes and their associated metrics can be created.

One goal of this literature review and the DST is to help integrate climate change considerations into restoration efforts. By planning and monitoring for resilience we are better able to document sources of adaptive capacity within restored and natural ecosystems. Therefore, it is important to determine if resilience planning can be integrated into existing restoration efforts and to define how it can be included. Should resilience be an assumed intention behind any restoration goal as Skidmore et al. (2013) suggests? Or would future restoration efforts benefit more if resilience was extracted from lofty goals and made into a discrete restoration or management objective?

From the literature review and management application process I have extracted three key points that may be helpful in answering such questions and integrating resilience measurements into restoration plans.

1. If made an explicit planning objective, as opposed to a component of existing objectives, resilience may be a way to improve restoration projects as a whole (Bisson et al. 2009; Thom et al. 2012).
2. Certain Ecological attributes are more widely supported to confer resilience within the literature.
3. Considering the projects ecological context and focal scale is essential in choosing appropriate resilience metrics to inform restoration efforts.

5.0 CONCLUSION

The need to accommodate for climate change in restoration design is becoming a common request among federal and state governmental agencies (WDFW 2013; O'Neal 2014). Many restoration projects are now required to evaluate the ability of a restored system or site to withstand impacts from climate change within their proposals and other planning documents. With growing regulatory and financial incentive to understand and increase ecological adaptive

capacity of restored sites, it is now more than ever, necessary for restoration practitioners to integrate resilience concepts into restoration planning and monitoring.

The dynamic nature of ecological systems is well known and the need to understand this feature is crucial for successful restoration work. How do degraded ecosystems recover and is the pathway to recovery similar to that of degradation? These are questions Suding and Gross put forward in 2006. Just as we should not assume continuous directional change in ecosystems so too should we avoid these assumptions in restoration efforts. Systems behave differently to disturbance and the assumptions made behind response and recovery trajectories can greatly influence restoration decisions. By monitoring a systems response and recovery we can better understand its potential for ecological resilience.

This study examined sources of ecological resilience to disturbances and clarifies one such way to increase available information on the adaptive capacity of a system to climate change impacts. In addition, a method is outlined for practitioners to identify appropriate resilience attributes for their restoration efforts. By reframing our approaches to restoration from creating optimal steady states to planning that incorporates and enhances natural sources of resilience, we may be better poised to adapt to impacts brought on by climate change. Future work in this field should focus on improving our understanding of how certain ecological attributes confer resilience. The challenge for managers is to evaluate the trade-offs that exist when selecting resilience of one ecosystem component over another and integrating a fundamental shift in how we manage our landscapes.

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APPENDIX: ATTRIBUTES AND CORRESPONDING SOURCES

The following table includes information detailing which articles were linked with individual attributes identified in this study.

	Grouped Attributes	Citation number
Individual Attributes	Individual growth rate	139, 151, 40, 8
	Individual size	59, 140, 157, 112, 37, 151, 173
	Life span	21, 40, 97, 161
	adaptability	188, 97, 94, 120, 63, 152, 180, 128, 96, 122
	Reproductive strategy	96, 144, 139, 63
	(Biological) adaptation to disturbance	152, 120, 21, 96, 180, 128, 69, 99, 185, 187, 94, 151, 121, 112
	Presence of propagules	121, 9, 45, 64, 3
	Dispersal potential	21, 123, 98, 40, 161, 63, 112, 182, 122, 85
	Efficient water capture and use	172, 102
Population Attributes	Genetic diversity	21, 184, 52, 142, 80, 111, 31, 183, 16
	Population size	96, 104, 115, 21, 108, 31, 16, 183
	Population density	152, 167, 59, 138, 35, 104, 115, 129, 82, 83
	Population growth rate	161
	Population age structure	111, 104, 26, 108
	Connectivity between populations	167, 21, 141, 42, 47, 31, 75, 118
	Population (beta) diversity	150, 78
Community Attributes	Community structure	43, 102, 173, 167
	Species assemblage	148, 62, 140, 84, 164, 145, 151, 182, 41, 186, 6, 21
	Species (alpha) diversity	188, 164, 61, 30, 49, 21, 2, 158, 102, 86, 29, 110, 92, 146, 171, 50
	Functional diversity	25, 166, 156, 18, 7, 153, 32, 168, 58, 102
	Response diversity	21, 72, 166, 7, 74, 56, 113
	Functional redundancy	21, 160, 38, 17, 166, 117, 175, 113
	Connectivity among communities	21, 134, 129, 116, 118, 22, 51
	Gamma diversity	168, 107
Ecosystem Attributes	Habitat area	130, 76, 42, 168, 167, 27, 4
	Habitat structure	167, 7, 24, 66, 43, 72
	Habitat condition	164, 27, 157, 169, 171, 140, 10, 44, 174, 190, 67, 129, 79, 1
	Temporal variability in habitats	27, 61, 22, 90, 87, 46, 105, 69, 162, 19
	Spatial variability in habitats	27, 151, 61, 22, 90, 112, 35, 164, 42, 46, 130, 39, 76, 105, 69, 171, 118, 162, 44, 36
	Refugia or support areas	37, 188, 27, 35, 163, 61, 90, 112, 33, 152, 111, 127, 8
	Connectivity between different habitats	188, 164, 22, 15, 42, 47, 126, 130, 118, 100, 116, 129, 111, 125, 168, 21, 136, 91
	Food web complexity	24, 57
	Large Woody Debris (LWD)	119
	Salinity	149
Process Attributes	Connectivity to refugia areas	188, 121, 112, 60, 186
	Energy flows	53, 94, 189, 24, 90, 169, 188, 39, 123, 149, 59, 65
	Release from competition or predation	21, 123, 55
	Sedimentation	106, 44, 159, 112
	Soil & air carbon balance	167, 174
	Hyporheic flows	119, 163
	Flow regime	97, 12, 5, 90
	Groundwater contributions	35, 27
	Structural legacies	21, 127, 45, 64, 114, 122, 140, 167, 3
	Water infiltration	23, 87
	Feedback between physical and biological processes	44, 101
	Recovery (time) after disturbance	121, 170, 186, 66, 152
	Natural disturbance history	145, 188, 121, 132, 148, 144, 68, 174, 53, 105, 180, 128, 103, 54, 98
	Random environmental variability	46, 118, 63, 139, 22, 162
	Disturbance duration and intensity	188, 121, 12, 93, 148, 84, 3, 140, 95, 81, 66, 149, 156
	Degree of exposure to human pressures	64, 105, 41, 48, 162
Historical flow-disturbance regimes	93, 14, 109, 182	

Table A1: Attributes by citation number as listed in references section