Ecological Restoration and Physiology: An Overdue Integration

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There is growing recognition that opportunities exist to use physiology as part of the conservation and management of populations and ecosystems. However, this idea has rarely been extended to the field of restoration ecology. Physiological metrics (e.g., gas exchange, energy transfer and metabolism, stress response, nutritional condition, gene expression) from a range of taxa can be used to understand the function of ecosystems as well as the factors that influence their structure. Such knowledge can assist the development and implementation of effective restoration strategies that recognize the role of habitat quality on organismal performance. Furthermore, physiological tools can be used to monitor the success of restoration projects during their implementation and as part of postproject monitoring. The often rapid response of physiological metrics provides more immediate information, enabling an adaptive approach to restoration, than can usually be obtained if the focus is solely on population- or ecosystem-level metrics. Greater integration of physiological responses into ecological restoration will provide practitioners with fundamental scientific information needed to design, implement, and monitor restoration activities to aid in repairing ecosystems around the globe.

Keywords: ecological restoration, physiology, environmental tolerances, monitoring, rehabilitation

Ecological restoration is increasingly being regarded as one of the primary means of repairing environmental damage caused by anthropogenic activities (Dobson et al. 1997, Hobbs and Harris 2001). Theoretically, ecological restoration implies that the historical ecosystem state is the objective, although in practice achieving that state is nearly impossible. Several approaches used in ecological restoration share the general goal of repairing damaged ecosystems but have different strategies and end points (Bradshaw 1987): rehabilitation (tends to focus on only part of the altered habitat), reclamation (rehabilitative work on severely disturbed habitat), recreation (construction of an alternative but nonetheless desirable state on a severely disturbed site where there was very little left to restore), enhancement (making ecological improvements), and mitigation or compensation (often focused on a different system). For the purposes of this article, all of these techniques fall in the broad category of "restoration ecology," the general aim of which is to restore both the structure and the function of degraded ecosystems.

In recent years a number of syntheses have outlined future directions and opportunities for restoration ecology (Allen 2003, Ormerod 2003, Young et al. 2005), emphasizing the need to adopt a more scientific approach to restoration relative to what was once regarded as an "art" (Van Diggelen et al. 2001, Davis and Slobodkin 2004). Although there has been a fundamental recognition that ecological and evolutionary theory and basic scientific research on ecosystem function are essential for providing a foundation for restoration (see Falk et al. 2006), little agreement exists on what constitutes a "successful" restoration project (Palmer et al. 2005). However, one element of ecosystem function—the physiological parameters of individuals—has received little attention in the context of restoration, despite the fact that understanding how a system works (i.e., how biotic and abiotic elements interact) is a prerequisite to effective conservation (MacMahon and Holl 2001). Indeed, in ecological restoration, knowledge of the cause of degradation and of the factors retarding restoration is essential; otherwise, those environmental factors that may be causing stress to ecosystems cannot be managed or regulated. Ricklefs and Wikelski (2002) introduced the concept of the "physiology/life-history nexus," wherein physiology is the key response mechanism linking both organism and population to their environment. Physiology can drive and constrain organismal responses to environmental pressures that ultimately structure ecosystems. Essentially, physiological

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regulation is directly responsible for the ability of an organism to adapt to new environmental conditions, such as those generated from degradation or restoration (Adolph 1956). In this context, physiology refers to regulatory mechanisms, performance (including growth and energetics), and environmental tolerances and their associated variability (Spicer and Gaston 1999). The underlying basis for physiological variation is widely thought to be genetic variation, both heritable and epistatic (Travis et al. 1999). Although physiology is often considered an end point (i.e., phenotype), it also serves as an indicator of underlying processes that are constituents of gene pools and their genetic variation. Thus, physiology is expressed as a measurable phenotype with direct connections to fitness (Feder et al. 2000).

New perspectives on the relationship between physiology and life history—and more broadly on the important role that physiology may play in evolutionary and ecological processes (Chown et al. 2004)—have been recognized for a number of taxa (Gutschick and BassiriRad 2003, Chown et al. 2004, Young et al. 2006). Recent work has highlighted the value of quantifying macrophysiology (the investigation of variation in physiological characteristics across populations over broad geographical and temporal scales) and demonstrating how it influences the evolution and ecology of target species (Chown et al. 2004, Osovitz and Hofmann 2007). Several studies have also documented that large-scale biotic and abiotic features (such as community composition and flow rate in the case of aquatic animals; light levels, water availability, and herbivory in the case of terrestrial plants) can dictate physiological characteristics of resident organisms (see Nelson et al. 2003, Ehleringer and Sandquist 2006, Kaufman et al. 2006). Moreover, there is growing recognition that many opportunities exist for integrating population- and individual-level physiological responses with traditional tools to help in the conservation and management of populations and ecosystems (Carey 2005, Stevenson 2006, Tracy et al. 2006, Wikelski and Cooke 2006). However, these ideas have not been extended to the field of restoration ecology or beyond vertebrates, save for a single paper on the physiological constraints on plants in a restoration context (Ehleringer and Sandquist 2006).

We aim to characterize the extent to which physiology has been used in ecological restoration, and to highlight potential opportunities to integrate knowledge of physiological responses into restoration efforts, using a well-known framework for ecological restoration (the Society for Ecological Restoration International's guidelines for ecological restoration). Although much of the fundamental research in ecological restoration has focused on plants, our approach is broader and includes all relevant taxa and systems. We also summarize the various physiological disciplines and their potential contributions to restoration ecology and discuss the challenges associated with integrating physiological knowledge into restoration projects. Finally, we present a research agenda to elucidate the future directions needed to integrate physiology and restoration ecology.

Current integration of physiology and ecological restoration

We conducted a systematic literature review (Pullin and Stewart 2006) to identify the extent to which physiology and ecological restoration were integrated. Initially, we searched for relevant articles that used physiological approaches in a manner that was specific to restoration ecology by evaluating only articles published in the leading journal in this field, *Restoration Ecology* (official journal of the Society of Ecological Restoration International, Blackwell Science Ltd., *www.blackwellpublishing.com/journal.asp?ref=1061-2971&site=1*). Using the Blackwell Synergy search engine, on 10 September 2007 we looked for the term "physiol*" in the text of every research paper published in *Restoration Ecology* from January 1997 to December 2006. Of the 620 research articles published during that period, 61 (10%) contained the string "physiol*" and used either physiological approaches or contained some discussion of physiology. However, many contained only a single use of the word "physiology." Relatively few studies actually incorporated physiological tools into their study design (n = 16). Rather, physiological information was used to provide context for the study, often justifying the choice of study organisms or helping to interpret study findings. Indeed, several papers explicitly called for supplementary physiological studies to provide a mechanistic understanding of observed patterns (e.g., why did one species have enhanced growth relative to another?). Most papers with physiological content (n = 47) focused on plants or on a combination of plants and their mycorrhizal associates (n = 4). Relatively few studies focused on animals; 4 focused on invertebrates, 1 on birds, 1 on fish, and 1 on mammals. Four articles focused on a combination of plants and animals. Of those studies centered on a specific environment, most dealt with terrestrial environments such as forests (n = 19), grasslands (n = 12), or arid environments (n = 4), whereas 13 papers focused on aquatic, wetland, riparian, and coastal environments. There were no clear temporal trends with a range in papers per year—2 in 2001 to a high of 9 in 2004 and an average of 6.1 per year—indicating that the use of physiological tools or information for ecological restoration is not currently increasing.

Next, we supplemented the focused search in *Restoration Ecology* with a more global literature review using the ISI Web of Science. The search was conducted on 30 September 2007 and included all available years. After initial trials, we selected the search term "ecolog*" and then, within those results, searched for the combined use of "physiol* and restor*". This approach yielded 78 records, 38 of which were determined (by a single reviewer) to be directly relevant to restoration physiology. The only trend of note uncovered by this global search was that restoration studies focused more on animals than on plants or environments, which suggests that much of this work is published in outlets other than *Restoration Ecology.*

Using the combined suite of papers generated from these searches, we qualitatively evaluated the literature to identify existing applications of physiology in the realm of ecological restoration. One of the most common themes, although not specific to restoration, is the need to identify the stressors contributing to a problem and determine the extent to which they are affecting organismal, population, and system levels. Indeed, this topic falls within the realm of "conservation physiology" and has been addressed elsewhere (Wikelski and Cooke 2006). However, it is worth noting that this is an important prerequisite to implementing any restoration plans. So far, the only synthesis on ecological restoration that includes a strong physiological perspective on the ecophysiological constraints on plant responses to restoration was written by Ehleringer and Sandquist (2006); in that paper, the authors emphasized the utility of physiological tools for identifying stressors in both above- and belowground processes.

A common theme among the studies that we located was using physiological information to enhance the effectiveness of biocontrol for invasive plant species (D'Antonio and Meyerson 2002). For example, Adams and Galatowitsch (2006) used studies of carbohydrate metabolism in the invasive reed canary grass (*Phalaris arundinacea*) in wet-meadow environments to reveal late-season storage of carbohydrates in rhizomes. Given that systemic herbicides are typically translocated to rhizomes through carbohydrates, this information provided a means to enhance the effectiveness of herbicide use through late-season applications.

Another common area of research that has benefited from physiological information is the study of metallophytes, which have the ability to tolerate extreme metal concentrations and thus are potentially suitable for the revegetation of mines and metal-contaminated sites. Although phytoremediation is reasonably well studied (reviewed in Salt et al. 1998), little is known about the physiological, molecular, and genetic mechanisms of metal hyperaccumulating metallophytes (Whiting et al. 2004). Such information is crucial for determining whether genetic modifications to metallophytes could enhance their utility for the remediation of contaminated lands. Dua and colleagues (2002) suggested that selecting the most appropriate bioremediation strategy (e.g., using microbes or plants) to treat a specific degraded site can be guided by considering three basic principles: the amenability of the pollutant to biological transformation to less toxic products (biochemistry), the accessibility of the contaminant to microorganisms (bioavailability), and the opportunity for optimization of biological activity (bioactivity). Clearly, fundamental understanding of organismal physiology is required for successful bioremediation within the context of ecological restoration.

One of the more studied topics relative to physiology and restoration concerns fire as a restoration approach for savannah-woodland habitats. Wallin and colleagues (2004) determined that for ponderosa pine (*Pinus ponderosa*), the benefits (in terms of leaf physiology and insect resistance) of restoration strategies such as burning and thinning were still evident seven years posttreatment. Similarly, Varner and colleagues (2005) summarized the physiological stress (on longleaf pine, *Pinus palustris*) associated with the reintroduction of fire regimes and identified a number of research topics, emphasizing the need for a mechanistic framework that would link physiological response to specific tree damage, and characteristics of the fuels and fire that caused the damage.

Studies that incorporate physiological information into models are widely used in ecology, but rarely have they been applied in a restoration context. A notable exception was the development of a physiologically based model for carbon dioxide (CO_2) exchange to evaluate the effects of water-level variation on CO_2 balance (as a proxy for ecosystem function) during the early phases of restoration in a cutaway peatland with *Sphagnum* reintroduction (Tuittila et al. 2004). The model revealed that *Sphagnum* was sensitive to fluctuations in water level, and therefore companion plantings were needed to expedite the ability of peatlands to serve as a carbon sink. The authors also noted that their ecophysiological model incorporated some assumptions about the variability of the system that were not relevant in practice. To be sure, there is still much room for validation studies. For example, Ahn and colleagues (2007) noted the need for experimental or field studies on seedling physiology to improve their dynamic model for predicting the recruitment and early survival of black willow (*Salix nigra*) in response to different hydrologic conditions in degraded riparian systems.

As noted above, many studies used knowledge of the physiological traits of a species to identify relevant study models and contrasted the performance of different organisms for various restoration applications. For example, Vance and colleagues (2003) used two common salt marsh plant species with contrasting physiology (*Salicornia virginica* and *Frankenia grandifolia*) to evaluate the potential of using sewage sludge to enhance soil nutrient levels in degraded salt marsh habitats. The authors determined that both species performed well (in terms of growth and survival) with the addition of sewage sludge, so other species with intermediate physiological traits relative to their two disparate models would also be likely to perform well.

In a similar study, Chen and colleagues (2005) compared the physiology of several tree and shrub species in ungrazed, overgrazed, and restored plots. The authors found relationships between the physiological properties of a species (its photosynthetic capability, e.g.) and the species' competitive advantage in different land-use types. In addition, the authors suggested that variation in the physiological characteristics of plants could explain the changes in species composition during degradation and restoration. Alterations in water tables can lead to problems with surface vegetation, and restoration plans therefore must incorporate information on the physiological consequences of different water levels on key plant species. Additionally, Chen and colleagues (2006) manipulated groundwater levels and assessed the physiological responses (on soluble sugars, endogenous hormones) of several tree species to identify minimum water-table levels needed to support unstressed, endemic tree species along the Tarim River in China. Finally, when restoring degraded sea grass beds, Orth and colleagues (2000) noted that knowledge of seed dormancy and germination physiology was crucial to the development of restoration plans. Thus, several restoration studies have benefited from knowledge of the physiological properties of their study organisms.

Researchers have also exploited the physiological benefits of mycorrhizae to enhance the restoration of desirable plant species. For example, Walker and colleagues (2004) determined that induced mycorrhization of sweet birch (*Betula lenta*) provided physiological benefits related to water uptake and nutrition that enabled the trees to flourish on harsh substrates (e.g., surface mine spoils) without intense application of chemical fertilizers. Elsewhere, researchers have used plant physiological traits as predictors of performance in restoration. Pywell and colleagues (2003) presented the results of a meta-analysis that evaluated the performance of plant species in restored vegetation communities throughout Great Britain. They noted variation in species performance that was related to 38 physiological and morphological traits. However, only a few species exhibited good performance across multiple sites, so focusing only on those species would facilitate revegetation but also would promote low diversity.

Overall, there are fewer examples of physiologically enhanced restoration on taxa other than plants, although there are some notable exceptions. For example, Ammar and colleagues (2000) used molecular physiology (expression of metabolic enzymes) to identify "unstressed" sites on coral reefs for use in restoration transplant efforts in the Red Sea. The octocoral *Dendronephthya klunzingeri* from the unstressed sites had substantially better survival and growth than those taken from sites identified as stressed. In wildlife realms, restoration plans often require the translocation of organisms from one area to another. Physiological knowledge can help ensure that stress from translocation is minimal so that introductions have a greater chance of success (reviewed in Teixeira et al. 2007). In river restoration and conservation efforts in Europe, Schiemer and colleagues (2003) have advocated that physiological studies focus on all life stages of the focal species. Recruitment bottlenecks for the threatened *Chondrostoma nasus* (a teleost fish) were attributed largely to physiological intolerances associated with river degradation and altered flow regimes, but these problems did not adversely affect the adults. A recent analysis of imperiled mammals in Australia concluded that habitat restoration projects must provide refuges from physiological stressors (i.e., disturbance, environmental extremes; McKenzie et al. 2007). In a similar example, Webb and Shine (1998) used information on the thermal physiology of an endangered snake in Australia to predict its critical habitat needs and to identify sites that could be restored to provide that habitat.

Even fewer studies of restoration physiology have been performed using multiple taxa. Adams and colleagues (2005) investigated the mechanisms associated with the recovery of fish and invertebrate diversity in a previously polluted system. Over a 15-year period, they noted decreases in contaminants, followed closely by an improvement in physiological and organismal-level indicators, improvements in fish and invertebrate community structure, and enhancement of the the periphyton community's chlorophyll *a* biomass and photosynthesis rate. Collectively, their results emphasize that field studies to assess and evaluate the effectiveness of restoration activities ideally should incorporate a variety of response end points ranging from sensitive and short-term responses (e.g., organismal physiology) to long-term but ecologically relevant indicators of change of aquatic ecosystems. It has also been suggested that it is possible to exploit the physiological state of animals to aid conservation strategies in plant communities (Rook and Tallowin 2003). Rook and Tallowin (2003) propose that knowledge of grazing-animal physiology can benefit grassland biodiversity by allowing manipulation of the grazing area.

Opportunities for integrating physiology and ecological restoration

In addition to the work described above are a number of opportunities for incorporating physiological tools and information in future restoration efforts. Such integration could benefit practitioners as well as advance the science of restoration.

To highlight the role of physiology for restoration practitioners, we used the Society for Ecological Restoration International guidelines that are suggested for conceiving, organizing, conducting, and assessing ecological restoration projects to identify opportunities for incorporating physiology into different restoration projects (see *www.ser.org/content/guidelines_ecological_restoration.asp*). These guidelines have been widely adopted and are applicable to any ecosystem, terrestrial or aquatic. The guidelines cover five general topics—conceptual planning, preliminary tasks, implementation planning, implementation tasks, and postimplementation tasks—and are directed toward restoration practitioners. As shown in table 1, there were many potential opportunities for using physiology to aid in planning, executing, and evaluating restoration projects.

Physiological tools can often yield data at a temporal scale that enables decisionmaking to occur during projects. Indeed, physiological responses often occur quickly, so response times may better suit the short monitoring periods typical of restoration projects. Physiological tools also enable reevaluation of progress so that restoration efforts can be adaptive instead waiting until after a program is successful to assess and revise a restoration plan. Often, physiology can detect subtle changes that would be difficult to find in the short term using classical ecological techniques (e.g., population demography, community structure). For example, if a long-lived species were living in a degraded system, it could be many years before one noted actual declines or recovery at the population level; but in considerably shorter time periods, physiological studies focused on the reproductive system could identify potential problems or successes with restoration efforts. Interestingly, we found no examples in the peer-reviewed literature where such an adaptive decision was

Table 1. Evaluation of guidelines from the Society for Ecological Restoration International that are relevant to the development of restoration projects that offer opportunities for integrating physiological techniques and information.

SER guideline for developing restoration projects	Opportunities for integration with physiology
3. Identify the need for ecological restoration	Although the focus is on identifying the broad factors that may have contributed to ecosystem degradation, knowledge of physiological concepts could help identify problems that are associated with depressed organismal condition. Using physiological response variables could be another metric used to quantitatively assess individual and ecosystem health and condition.
5. Identify restoration goals	Goals are the ideal states and conditions that an ecological restoration effort attempts to achieve. Including goals associated with organismal physiology or condition (e.g., energetics, performance) can be quantified and thus provide tangible benchmarks by which success can be measured
6. Identify physical site conditions in need of repair	Many ecosystems in need of restoration are dysfunctional because of damage to the physical environment. Knowledge of organism-environment relationships (e.g., tolerances) that may influence demography can aid in identifying appropriate physical characteristics to target.
7. Identify stressors in need of regulation or reinitiation	Stress can be thought of at multiple levels (from ecosystem to the molecule). From a physiological perspective, a stressor is a factor that compromises the ability of an organism to maintain homeostasis. The physiological response of organisms to stressors can be quantified and used to determine the relative magnitude of different stressors.
8. Identify and list the kinds of biotic interventions that are needed	Removal or addition of biota in an effort to restore a system can benefit from knowledge of physiology. For example, introduction of mycorrhizal fungi or nitrogen-fixing bacteria (to play a physiological role) requires physiological knowledge about the organisms and their relationships. Similarly, to eradicate a species, knowledge of their physiology can be useful in identifying a life-cycle stage at which they are particularly sensitive to disturbance, or in pinpointing the mode of action of a pesticide.
9. Identify landscape restrictions	Population demographics of many species at a project site may be adversely affected by external conditions and activities offsite in the surrounding landscape. For example, in a watershed, one would have to work upstream in the catchment when trying to deal with a problem in a given reach. As with guideline 7, physiology can be used to determine which stressors are influencing the system, and thereby identify potential landscape restrictions.
10. Identify project funding sources	Inclusion of physiological approaches could provide additional opportunities for funding because of their novelty and potentially integrative nature.
12. Identify biotic resource needs and sources	Biotic resources (e.g., seeds, propagules, animals) may be needed for establishment or reintroduction at the project site. Knowledge of intraspecific differences in performance (i.e., local adaptation), as well as how to handle, transport, and introduce organisms in a manner that reduces stress, is essential to ensuring survival and potential reproduction.
17. Appoint a restoration practitioner who is in charge of all technical aspects of restoration	Restoration projects are complex, require the coordination of diverse activities, and demand numerous decisions owing in part to the complex nature of ecosystem development. Ensuring that the practitioner has knowledge of physiological concepts and principles to complement other skills will prove useful.

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made on the basis of physiological information. Assessing a restoration program's success is essential for determining the extent to which the restoration strategies, monitoring, and assessment tools can be extended to other systems. However, contemporary reviews that focus on measuring the effectiveness of restoration have failed to emphasize the role for physiology (e.g., Ruiz-Jaen and Aide 2005).

We identified a number of opportunities for incorporating physiological tools and information into the practice and science of ecological restoration. For example, ecophysiological models can predict the response of ecosystems to different restoration strategies, thus providing managers with better information for decisionmaking. Models must be parameterized with basic information of organism-environment relationships that have a physiological basis. Models can also help researchers understand causal relationships and the mechanistic processes among environmental stressors, stress responses of biota, and the recovery processes (Adams et al. 2005).

Physiology also has the potential to contribute to the assessment of habitat quality. Huey (1991) wrote the first basic synthesis on the relationship between habitat quality and organismal condition. More recently, there has been applied interest in understanding how organisms respond to different habitats. Indeed, at some level, the relationships among habitat quality, organismal condition, and fitness are fundamental to field of restoration ecology.

When conducting restoration projects, the incorporation of physiological dynamics into the planning and evaluating of projects has been recently lauded (Gardmark et al. 2003). This approach is particularly relevant to the selection of appropriate reference sites (White and Walker 1997, Ehleringer and Sandquist 2006). Recovering populations can exhibit altered physiological traits, the consequences of which are unknown (Gardmark et al. 2003). However, modeling, combined with empirical research, would be a productive research topic for predicting and understanding recovery dynamics. Because climate change is occurring rapidly, there is also an urgent need to understand how ecosystems will respond. As restoration attempts to hit a moving target (i.e., the desired ecosystem target for restoration is not static), physiological information may help to reveal the under-

Table 1. (continued)

SER guideline for developing restoration projects	Opportunities for integration with physiology
20. Document existing project site conditions and describe the biota	Comprehensive and detailed assessment (including species distribution and abundance) that quantifies the degree of degradation (including stress) or damage. Although there is much emphasis on structure, functional elements are also relevant. In particular, physiological metrics can be quantified for later evaluation to contrast the project site and its inhabitants before and after restoration.
22. Conduct preproject monitoring as needed	Baseline measurements could include physiological metrics such as gross metabolism of soil organisms, leaf photosynthetic activity, or animal corticosteroid levels. It would be impractical to monitor these activities on all organisms or ecosystem components, but it is possible to select representative metrics that could be measured throughout the life of the project. Because physiological tools have the potential to provide data immediately, these tools could enable adaptive changes in project design.
23. Establish the reference ecosystem	The reference model represents the future condition or target on which restoration is designed, and will later serve as a basis for project evaluation. Long-term physiological monitoring programs have the potential to be used in a reference context.
24. Gather pertinent autecological information for key species	Information on basic life-history and environmental relations is needed before initiating any restoration project.
25. Conduct investigations as needed to assess the effectiveness of restoration methods and strategies	With increased use of innovative restoration methods, there is a need to test different strategies before their implementation at a project site. Physiological tools can be used in an experimental setting or in small-scale pilot projects to demonstrate feasibility or reveal weaknesses in restoration design and execution before attempting larger-scale restoration.
27. Prepare a list of objectives designed to achieve restoration goals	Physiological endpoints can be used as objectives. For example, an objective when restoring degraded forests might be to achieve a self-sustaining population of a given tree species. This could be taken further to include a physiological component dealing with the nutritional physiology of the tree (e.g., to strive to ensure that the nutritional physiology of trees at the site is similar to that of trees at an appropriate reference site).
33. Engage and train personnel who will supervise and conduct project implementation tasks	Some personnel may require specialized training. However, it is most likely that any physiological tools would require collaboration with a physiologist who could share his or her expertise with other team members.
36. Prepare performance standards and monitoring protocols	Related to guideline 27, performance standards detail a specific state of ecosystem recovery that indicates or demonstrates that an objective has been attained.
46. Perform monitoring to document the attainment of performance standards	Physiological monitoring can occur before, during, and after restoration.
47. Implement adaptive management procedures	Because physiological responses tend to be more rapid than other metrics, physiological monitoring can enable adaptive changes during project implementation.
48. Assess monitoring data to determine whether performance standards are met and project objectives are attained	Physiological tools can provide unique insight into the mechanisms underlying successful or failed projects.
51. Publicize and prepare written accounts of the completed restoration project	As documented in this review, there are few published examples of physiological tools being used in the field of restoration ecology. There is therefore a need to publish these studies in the primary literature.

SER, Society for Ecological Restoration.

Note: The guidelines evaluated are from version 2, updated in December 2005 and downloaded on 10 October 2007. Numbers correspond to the SER guidelines; only those guidelines for which physiology is relevant are listed.

pinning of how organismal tolerances will change (Lavendel 2003).

Knowledge of physiology can aid in determining which species and stocks should be used for reintroductions or plantings in degraded areas. Montalvo and colleagues (1997) considered the potential role of population biology in restoration ecology and suggested that local adaptation and variation in life history traits required study. In general, the use of locally adapted populations for restoration projects promotes better performance and higher fitness (Bradshaw 1984). Interestingly, experimental approaches to restoration also provide opportunities to generate fundamental understanding of the extent to which phonological, morphological, or physiological differences affect ecological services and functions (such as herbivory, pollinator visitation, fruit initiation, seed set, and seed predation of plants; Montalvo et al. 1997). Similarly, Van Andel (1998) conducted a synthesis on intraspecific variability in the context of ecological restoration and addressed whether knowledge of organismal responses to environmental factors (e.g., pH, nutritional status, pollutants, temperature) is sufficient to estimate the chances of reintroduction and restoration success. The author argued that transplant studies were needed to provide knowledge on choice of organisms (e.g., which source population and whether multiple sources are preferable to a singe source) for restoration projects. However, Van Andel (1998) also suggested that the easiest way to provide the best chance of success for restoration projects in variable environments was to use organisms from multiple sources.

The final opportunity that we noted was that additional restoration physiology studies must be performed using species other than plants. Furthermore, few studies that use physiological end points or knowledge focus on more than one species. Multitaxon physiological studies are needed to better represent different ecosystem elements and to better understand overall function. We are aware of only a few studies that have looked at physiological metrics in multiple taxa simultaneously, even though this approach would enable a mechanistic assessment of the structure and function of degraded or restored ecosystems (Adams et al. 2005).

Challenges with integrating physiology and ecological restoration

There are a number of actual or perceived challenges to the integration of physiology and ecological restoration. Most deal with what we regard as a lack of knowledge about what physiology can offer to the field of ecological restoration and about how the integration of the two fields can be achieved technically and practically. One of the primary challenges to incorporating physiological parameters into restoration efforts is the assumption that physiological techniques are limited to laboratory environments (see table 2 for a summary of physiological techniques and their potential value in restoration projects). In recent years, many developments have allowed physiological techniques to be transferred from the laboratory to field environments, giving rise to an emerging discipline called "field physiology" (Costa and Sinervo 2004, Goldstein and Pinshow 2006). At one time, physiological equipment was cumbersome and time sensitive, but now a number of tools and techniques specially designed for field applications are available. For example, to evaluate plant physiology in the field, lightweight portable gas-exchange systems (at several scales) have been developed, as have compact data loggers that can be deployed in remote locations for extended periods of time (Ehleringer and Sandquist 2006). For animals, advances in biotelemetry and biologging techniques enable monitoring of free-ranging animals with sensors that record, for example, heart rate, flipper or tail beats, temperature, and depth (Cooke et al. 2004). There is also a growing number of portable devices that enable one to perform respirometry with mobile devices or to use portable analytical devices to assess blood biochemistry and hematology in near real time (e.g., glucose, lactate, ions, blood gasses, hematocrit). Proxies such as stable isotopes and doubly labeled water, which provide an integrated perspective on ecophysiological performance (see Costa and Sinervo 2004, Goldstein and

Table 2. Examples of physiological disciplines and their potential contributions to restoration ecology.

Physiological discipline	Tool (examples)	Potential contribution to restoration physiology
Physiological genomics and proteomics	Gene expression profiling using DNA microarrays; quantitative PCR; quantitative protein-level measurements of gene expression	Monitor the expression levels of genes associated with the presence or absence of different stressors and such knowledge can be used to predict responses to restoration; identify genes and genetic variation underlying complex physiological traits; genetic modification can help "design" organisms (e.g., metallophytes) to use in the remediation of contaminated land/water
Environmental toxicology	Bioremediation (microbial, phyto); quantification of trace elements; experimental tests of negative health effects	Provides information on the physiological effects of different environmental contaminants on organisms to help identify candidate organisms for bioremediation; can help determine when a site has been remediated or when restoration efforts have been "successful"
Endocrinology	Blood sampling or noninvasive collection of animal feces; tissue sampling of plants	Enables quantification of anthropogenically induced chronic or acute stressors (e.g., relative to different habitat qualities) that can ultimately affect fitness or survival; provides information on the reproductive biology of organisms (offspring, fruit) that can be used for captive breeding (for replanting or releases), biological control, or to quantify population growth or decline
Evolutionary physiology	Theoretical models	Links life history, population biology, and fate of organisms; develops models to predict the long-term evolutionary consequences of selection for different phenotypes and their potential response to different environmental change (including degradation and restoration)
Immunology and epidemiology	Tests for the functioning of systemic innate, cell-mediated or humoral immune responses; pathogen infection (bacterial, viral, fungal); production of reactive oxygen/nitrogen species	Can quantify pathogen infection or a population's susceptibility in a given habitat to aid in selecting appropriate cultivars/populations for restoration; aids in understanding responses to pathogens, which can be useful in population viability analyses; can help understanding of how plants and animals define and defend self against nonself (parasites and microbial pathogens); can be combined with "evolutionary physiology" to understand how immune mechanisms have evolved in response to new pathogens and environmental challenges
Environmental and ecological physiology	Gas exchange/respiration studies (individual plants through to ecosystem level); microbial and mycorhyzal physiology; biotelemetry and biologging tools to quantify body temperature, energy expenditure, or activity; doubly labeled water; nutrition and lipid analysis; response of organisms to extreme conditions; monitoring of climate/weather and habitat quality	Allows the generation of models to predict the response (growth, fitness, survival) of organisms to different stressors and restoration plans; enables the selection of appropriate organisms (populations and species) for restoration; helps describe organism distributions relative to habitats of differing quality; enables the evaluation of restoration success by monitoring organismal function relative to environmental conditions; energetic and gas exchange studies can be translated to systems-level measures of ecosystem function, thus connecting individual physiology with "higher-level" restoration goals

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Table 2. (continued)

Physiological discipline	Tool (examples)	Potential contribution to restoration physiology
Developmental physiology	Event sequences (heterochrony and heterokairy); describes the onset and progression of physiological regulation; physiological investigation down to the embryonic level	Focuses on how developing physiological systems are directed by genes yet respond to environment and how these characteristics both constrain and enable evolution of physiological characters (Burggren and Warburton 2005); aids understanding of how physiological systems and whole organisms develop and how populations evolve in the face of different environmental conditions; offers opportunities for using genetic engineering to develop organisms that can be used in bioremediation or that can survive in degraded sites; helps understanding of the habitat and environmental needs of organisms during the often sensitive early stages of their development, which can be used in restoration planning and monitoring
Comparative physiology and biochemistry	Enzyme activity assays; determination of reactive oxygen species; production of proteins (e.g., heat shock); cellular metabolism	Assesses impact of stressors on individuals in a population or on species in a population to understand how they will respond to different restoration scenarios; develops relationships that can be used to predict how organisms and populations respond to stressors and restoration
Neurophysiology and sensory biology	Direct neuropeptide manipulations in wild animals; neuroregulators and neurotoxins in plants; biotelemetry of neural activities; neurotransmitters	Aids understanding of communication in plants from molecules to ecosystems to ensure that biotic interactions are incorporated and understood in restoration projects; facilitates understanding of the neural basis of behaviors, making it possible to learn why animals are using or avoiding different habitats; helps understanding of how organisms sense and evaluate habitat quality

Note: The disciplines roughly follow those listed by Wikelski and Cooke (2006) for a more generic evaluation of the physiological disciplines relevant to the conservation of vertebrates.

Pinshow 2006), can be quantified relatively easily with field-collected samples.

As ecologists and physiologists try to close the gap between laboratory and field research, even more tools relevant to the field of ecological restoration will become available. It is important to note that these tools require validation and testing before they are ready for use in a restoration project.

Associated with the presumed lack of equipment is the assumption that physiological assessments are expensive. Of course, capital equipment, such as a respirometry system, may sometimes need to be purchased, but in many cases physiological tools provide good value because response times are quick and often obviate the need for extensive field-sampling programs. Hence, careful budgeting is needed to project the cost of incorporating physiological approaches into a restoration program.

One way to reduce cost is through collaboration. Indeed, collaboration also ensures that a project receives needed technical and analytical expertise, given that many practitioners of ecological restoration do not have extensive training in physiology or biochemistry. Restoration ecologists need additional training, however—which could perhaps be offered through professional societies—to learn to recognize the many opportunities that exist for working in concert with physiologists. Likewise, in a research context physiologists need to be encouraged to develop and apply techniques that have relevance to ecological restoration. Examples of restoration research or projects that incorporate physiology should be disseminated to the scientific and application communities through publication of case studies and papers in peer-reviewed outlets. Failures and successes of restoration work that incorporates physiology should receive equal emphasis: instances in which physiology failed to provide needed information should get as much attention as instances in which it did.

Reasonably few restoration studies have integrated information from the molecule to the ecosystem, although several recent syntheses have noted that such approaches are required to understand water needs and flood tolerances of plants (Blom 1999), forest restoration potential (Rajora and Mosseler 2001), remediation of contaminated sites (Vasseur and Cossu-Leguille 2003), and the complexity of responses seen during restoration (Gardmark et al. 2003). One of the biggest challenges to such an approach is that physiology tends to focus on molecules, organs, and individuals. So how can physiological research be reconciled with an ecosystem perspective? As Ehrenfeld and Toth (1997) noted, ecosystem function must be considered in restoration projects, and many of these functions, as well as basic ecological theory, have a basis in physiology (Odum 1969). Indeed, even ecosystem structure can be influenced by the physiological tolerances of resident species.

Undoubtedly challenges will arise when translating physiological processes to the population, community, and ecosystem levels, but the links are now clear between physiology and demographic processes (i.e., the physiology–life history nexus; Ricklefs and Wikelski 2002). Moreover, understanding of how organismal stress relates to ecological and evolutionary processes is now reasonably well understood (Calow and Forbes 1998). Because physiology tends to focus on individual organisms, it is common to document extensive individual variation, a characteristic that was once regarded as "statistical noise" (Bennett 1987) but is now regarded as an interesting and fundamentally important element of biology. Carey (2005) argues that the study of such variation will become even more critical in the effort to understand how environmental stressors influence organismal survival; this idea can easily be extended to an effort to understand how organisms will respond to different restoration scenarios. Of course, individual variation can also present challenges for interpreting data, and requires extensive knowledge of the spatial-temporal scale and other factors relevant to such variation in organismal condition.

It is also worth noting that not all restoration is focused on the ecosystem level. For example, some activities focus on a single species, taxonomic group (e.g., plants), or type of organism (e.g., commercially valuable fish species). These projects, or even those with a clear ecosystem perspective, could use information from individuals as a proxy or sentinel for ecosystem performance and function. For a study on stream restoration, for example, one could decide to study the physiological and energetic condition of an indicator species such as sculpin or a salmonid. A more robust approach may be to evaluate physiological responses in a suite of representative sentinel species that could include multiple functional levels in a food chain or web (e.g., producers, first-order consumers, second-order consumers, decomposers), as has been proposed by Depledge and Galloway (2005). In some ways, these sentinel approaches assume a link between habitat quality and organismal physiology. Although the number of empirical examples of these theorized links (reviewed in Huey 1991) is growing, there is clearly still a need for additional research on this topic across different ecosystems and using different proxies. The single-species approach and the ecosystem-oriented approach each have strengths and limitations, and greater integration of the two and synergies arising from it would make it possible to parlay the benefits of both (Lindenmayer et al. 2007).

Conclusion and research agenda

Our synthesis shows that some attempts have been made to use physiological tools and knowledge to enhance the science and practice of restoration ecology. In general, however, the integration of physiology and restoration ecology has not been fully realized. We contend that physiological tools and knowledge have much to offer the field of ecological restoration, providing restoration practitioners with fundamental scientific information needed to design, implement, and monitor restoration activities to aid in repairing ecosystems around the globe (table 3). Before this integration can be fully realized, more research that brings basic biology together with applied restoration questions is necessary. Indeed, there are numerous taxa and systems for which knowledge of organismal

Table 3. Comparison of the advantages and limitations of the physiological approach and more traditional systems-level approaches to ecological restoration.

Perspective on approaches	Physiological approach	Traditional approach
Advantage	Measurement is focused on organisms, the fundamental building blocks of populations, and can include fitness and health indicators	Measurement of the success of restoration is focused on populations and communities, which are integrative in nature
	Rapid response time for evaluating changes in organismal stress and condition	Current trend in ecological restoration to focus on the ecosystem level is more consistent with traditional measurements
	Conducive to complementary lab or mesocosm studies to provide detailed information on mechanisms that are driving patterns of abundance and distribution	Practitioners and regulators are trained in and familiar with the collection and use of traditional metrics in ecological restoration
	Provides useful information that can be modeled to predict organismal-level responses to different restoration scenarios	Many of the data collection techniques can be done without actually handling, killing, or removing organisms from their habitat
	Provides information on organismal tolerances needed for informed (re)introduction or captive breeding programs	Focus is on the function of the system rather than the structure
Limitation	Relationship between organismal stress and higher-level processes (e.g., population dynamics) poorly understood	Measurements at higher levels of biological organizations do not provide information relative to the mechanisms or cause of changes at the population or community level
	Regulators and practitioners will require training in physiological concepts and techniques if these tools are to be used in an applied context	Sampling is often laborious and needs to extend across multiple years (long term), as response variables (e.g., community structure) can be slow to respond; this is often inconsistent with short-term monitoring budgets
	Although most sampling on animals is not lethal, it does require some semi-invasive procedures (e.g., blood sampling), which may not be permitted on endangered organisms	Focus on structure, not function of a system
	Inherent high levels of individual variability require knowledge of the spatiotemporal scale and baseline condition of organism	
	Metrics such as stress indices can be too sensitive, so more integrative measures related to metabolism and energy allocation must be included	

physiology and environmental relationships is simply insufficient to predict and accomplish successful restoration (e.g., seagrass, Thorhaug 1990; wetlands, Zedler 2000; metallophytes, Whiting et al. 2004). We need more research devoted to the development and validation of ecophysiological models for use in ecological restoration, particularly those that enhance predictive capacity and recognize system (abiotic and biotic) dynamics during periods of degradation and restoration (see Gardmark et al. 2003). There are also many opportunities to combine laboratory and field approaches in physiology to experimentally evaluate the candidacy of different species and populations for use in reintroduction or planting projects, and several such studies have already been published and have been used by restoration practitioners.

The technical aspects of using physiological tools in the field still require more work, but more and more tools and techniques are being developed or adapted for field studies (Costa and Sinervo 2004). Research techniques and tools that are especially promising include those that deal with physiological genomics (cDNA gene microarrays) and proteomics, which have much to offer ecological restoration, including the ability to predict how different populations will respond to stressors (Klaper and Thomas 2004, Thomas and Klaper 2004, Ryder 2005). Although many of the gene arrays developed to date focus on experimental organisms (*Arabodopsis,* mice, humans, *Drosophila*), there is a growing trend toward the development of gene arrays for more ecologically relevant models that would be useful for restoration planning (e.g., salmonids, von Schalburg et al. 2005; sea grasses, Procaccinia et al. 2007). In addition, genomics may reveal opportunities for potentially using genetic engineering to establish populations that are tailored to life in highly degraded systems (Vasseur and Cossu-Leguille 2003).

This integration presents challenges, in that physiology tends to focus on individuals and populations, whereas ecological restoration tends to focus on ecosystems. However, physiological metrics focused on a suite of organisms (i.e., multiple taxa; Depledge and Galloway 2005) can yield information on the function of ecosystems (Calow and Sibly 1990, Lindenmayer et al. 2007) and serve as proxies for monitoring the success of restoration programs across timescales consistent with the relatively short monitoring periods—short because of budgetary constraints—typical of restoration projects. Studies that compare the use of physiological metrics and more conventional population- and community-level indicators for the assessment of restoration success across multiple spatial and temporal scales would be extremely useful for understanding the relative strengths and weaknesses of each approach. In addition, an ecological community has some characters that are not a consequence of individual processes but are an epiphenomenon of complexity; it is unclear how or even if physiology can contribute to this conceptual arena, although there may be opportunities for integrative modeling approaches. Also needed is more fundamental research devoted to evaluating the relationship between habitat quality and organismal condition and performance, and the extent to which organismal condition and performance are correlated with population demography.

To effectively integrate physiology with restoration ecology, the restoration ecology community must recognize that physiology is not an irrelevant discipline or tool. One way to achieve this systemic recognition is to educate restoration practitioners about the merits of physiological tools by publishing both successful and failed instances in which physiology has been used in restoration projects; professional societies could help in this endeavor by organizing workshops and symposia on the topic. Efforts to restore degraded ecosystems around the globe require the collective creativity and knowledge of experts with varied training and from different disciplines (including physiology) if practitioners are to gain the fundamental scientific information they need to design, implement, and monitor restoration activities. The integration of ecological restoration and physiology is overdue. So far, examples of successful integration are few, but the opportunities for it are many.

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