RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

ADVANCES IN MINING RESTORATION

REVIEW ARTICLE

Leveraging the value of conservation physiology for ecological restoration

Sean Tomlinson[1,2,3,4], Emily P. Tudor[2,3,5], Shane R. Turner[3,5,6], Sophie Cross[6], Fiamma Riviera[5,6], Jason Stevens[3,5,6], Justin Valliere[7], Wolfgang Lewandrowski[3,5]

The incorporation of conservation physiology into environmental management, particularly ecological restoration, is underutilized, despite the capacity of such approaches to discern how populations respond to the challenges of unpredictable and potentially inhospitable environments. We explore several examples where detailed mechanistic understanding of the physiological constraints of keystone and foundational species, ecological service providers such as insect pollinators, and species of conservation concern has been used to optimize the return of these species to landscapes following the cessation of mineral extraction. Using such data can optimize the rapid return of functioning ecosystems during restoration or increase the conservation value of restoration by returning insurance populations of threatened species. Integrating this level of mechanistic understanding with fine-resolution spatial data in the form of biophysical modeling can help plan recovery and identify targets that can subsequently be used in assessing restoration success, particularly in situations that require substantial investment over long periods, such as post-mining restoration. There is growing recognition of the valuable insights offered by conservation physiology to broader practice and policy development, and there have been substantial technical developments in conservation physiology leading up to and into the twenty-first century as a result. The global challenge facing restoration ecology has, however, also grown in that time. Rapidly and efficiently meeting ambitious global restoration objectives will require a targeted approach, and we suggest that the application of physiological data will be most strategic for rare species, keystone species, and ecosystem service providers more broadly.

Key words: animal physiology, biodiversity, ecological restoration, ecophysiology, *ex situ* conservation, gene-banking, *in situ* conservation, niche modeling

Implications for Practice

- The constraints imposed by hostile restoration landscapes on the return of key groups or organisms essential to the return of functioning ecosystems (e.g. keystone or foundation species, or service providers) can be empirically understood by the collection of data on their physiological performances and tolerance thresholds.
- Integrating empirical data on physiological tolerances with microclimatic or other environmental data at high resolution via biophysical modeling can provide mechanistic insight into the constraints on key groups to guide restoration planning and monitoring.
- The costs implied by collecting such in-depth data can be strategically offset by increasing the successful return of keystone and foundation species, service providers, and rare species to restoration, optimizing the biodiversity conservation value of such enterprises.

Introduction

Physiology seeks the fundamental mechanisms of "how organisms work," both in response to manipulated scenarios *ex situ* and natural environments *in situ* (Somero 2011). Conservation physiology is an applied discipline, seeking to identify, diagnose, and address the decline of species and improve their management using physiological theory (Wikelski & Cooke 2006). This

Author contributions: ST, WL led the writing and developed the first draft; all authors made equal contributions to subsequent drafts; EPT, FR, WL developed Figure 1.
[Correction added on 8 September 2022 after first online publication: The copyright line was changed and legal statement was added.]

[1]School of Biological Sciences, University of Adelaide, North Terrace, Adelaide, South Australia 5000, Australia
[2]School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia 6102, Australia
[3]Department of Biodiversity, Conservation and Attractions, Kings Park Science, Kings Park, Western Australia 6005, Australia
[4]Address correspondence to S. Tomlinson, email sean.tomlinson@adelaide.edu.au
[5]School of Biological Sciences, University of Western Australia, Crawley, Western Australia 6009, Australia
[6]ARC Centre for Mine Site Restoration, School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia 6102, Australia
[7]Department of Biology, California State University Dominguez Hills, Carson, CA 90747, U.S.A.

doi: 10.1111/rec.13616

paradigm is underpinned by the expectation that, if physiological interactions between the organism and the environment (both biotic and abiotic) define the niche of a species (Hutchinson 1957), they can also be used to identify, understand, predict, and manage or mitigate threats to that niche (Wikelski & Cooke 2006). Conservation physiology ultimately seeks to determine the factors underpinning population persistence, to improve species preservation and the reinstatement of populations following degradation or disturbance (Cooke et al. 2013). Various aspects of environmental management, such as conservation biology, wildlife management, and restoration ecology are broadly focused on preserving and reestablishing functional biological communities (Young 2000). Conservation physiology, on the other hand, is a more defined approach to single species' ecology (usually of conservation concern), and their individual and unique physiological requirements for persistence (MacMahon & Holl 2001). While conservation physiology should not be viewed as a "silver bullet" for immediate restoration success, there are many examples integrating physiological data with ecological, behavioral, or genetic studies that advance ecological restoration and threatened species recovery (Cooke et al. 2021). Moreover, since the first calls for the integration of conservation physiology with restoration (Cooke & Suski 2008), the theory and techniques underpinning physiological research have advanced substantially. Using these tools, conservation physiology provides greater opportunity to improve environmental management of "at-risk" species, including their ecological restoration.

Physiological traits and constraints can drive organism responses to environmental pressures in ways that ultimately structure ecosystems (Cooke & Suski 2008). In the context of degraded landscapes, organisms are often exposed to extreme, novel environments that do not always provide conditions or resources that support all aspects of their function. Conservation physiology has recently explicitly identified research tools aimed at ameliorating these limitations to restore such degraded environments (Ehleringer & Sandquist 2006; Hay & Probert 2013; Cooke et al. 2021). However, much of the research that is suggested involves substantial investment in a small number of species, and the integration of such focused, mechanistic studies with the broader, ecosystem-level objectives of ecological restoration is often lacking.

We explore how strategic species selection and a niche-focused approach can provide insights for environmental management broadly, and ecological restoration in particular. The concept is broadly applicable, given the degree of rapid environmental change wrought by contemporary threats such as climate change, urbanization, industrialization, agricultural intensification, and mining (Tilman et al. 2017), and the increasing social, economic, and legislative demand for restoration following land degradation. Mine closure provides a particularly stark example of the challenges facing ecological restoration which could be constructively informed from a physiological perspective. As such, we draw on some examples of how post-mining ecological restoration can draw on physiology-based approaches to optimize species distribution modeling ("Biogeography"; Fig. 1), species' responses to changing environments ("Organismal physiology"; Fig. 1), species preservation under controlled scenarios ("*Ex situ* conservation"; Fig. 1), production of viable reintroduction populations ("Population production"; Fig. 1), and threat mitigation and conservation planning ("*In situ* assessment"; Fig. 1). We recognize that this is a highly intensive research paradigm, and that it is impractical to apply such high-resolution research to every species in a restoration assemblage. Instead, we suggest several key groups of organisms (Fig. 1) that merit detailed mechanistic understanding in ecological restoration. Accelerating the restitution of some groups might provide critical services to the reassembling ecosystem (such as pollinators—Menz et al. 2011; foundation species—Angelini et al. 2011; or keystone species—Hale & Koprowski 2018), and some may require specific, detailed attention (such as rare or threatened species—Volis 2019). We finally consider future integration of conservation physiology into broader ecological restoration, because the concepts that we explore here are applicable beyond the context of post-mining restoration.

Applications of Conservation Physiology in Ecological Restoration

Determining the Physiological Basis for Species' Distributions ("Biogeography")

High-resolution biogeographical models can guide site selection, assist development and monitoring for threatened species translocations and reintroductions, and foster better understanding of where mitigation efforts might be most effective (Tomlinson et al. 2019). Using biologically relevant environmental data, such models can identify landscape elements critical to the species, either in undisturbed locations, or those theoretically to be reconstructed during restoration (as is required following mining). High-resolution biogeographical models can be developed using proxies for microclimatic or microhabitat elements that shape the niche derived by remote sensing (Lannuzel et al. 2021). However, the distributions of many narrow-range endemic species, especially plants, can be more accurately modeled using edaphic features (Beauregard & De Blois 2014; White et al. 2020). While statistical, correlative models cannot provide direct insight into the physiological processes that might limit the ecological restoration of such species (Zurell et al. 2021), the inclusion of edaphic features can facilitate *post hoc* interrogation of the most limiting microclimatic factors for a species (Tomlinson et al. 2019). This level of interrogation offers some insight into the fundamental niche and physiological constraints of species, which may guide the selection of performance metrics (e.g. gas exchange, water relations, or metabolic rate) by which to infer restoration or translocation success (or lack thereof).

In contrast to correlative models, the growing field of mechanistic and/or process-based modeling can characterize the realized niche from physiological constraints delimiting the fundamental niche (Kearney & Porter 2017). Such models are increasingly used to identify threats and guide the recovery of ecological service providers or threatened fauna (Porter et al. 2006; Mitchell et al. 2013). For example, the return of insect pollinators to many

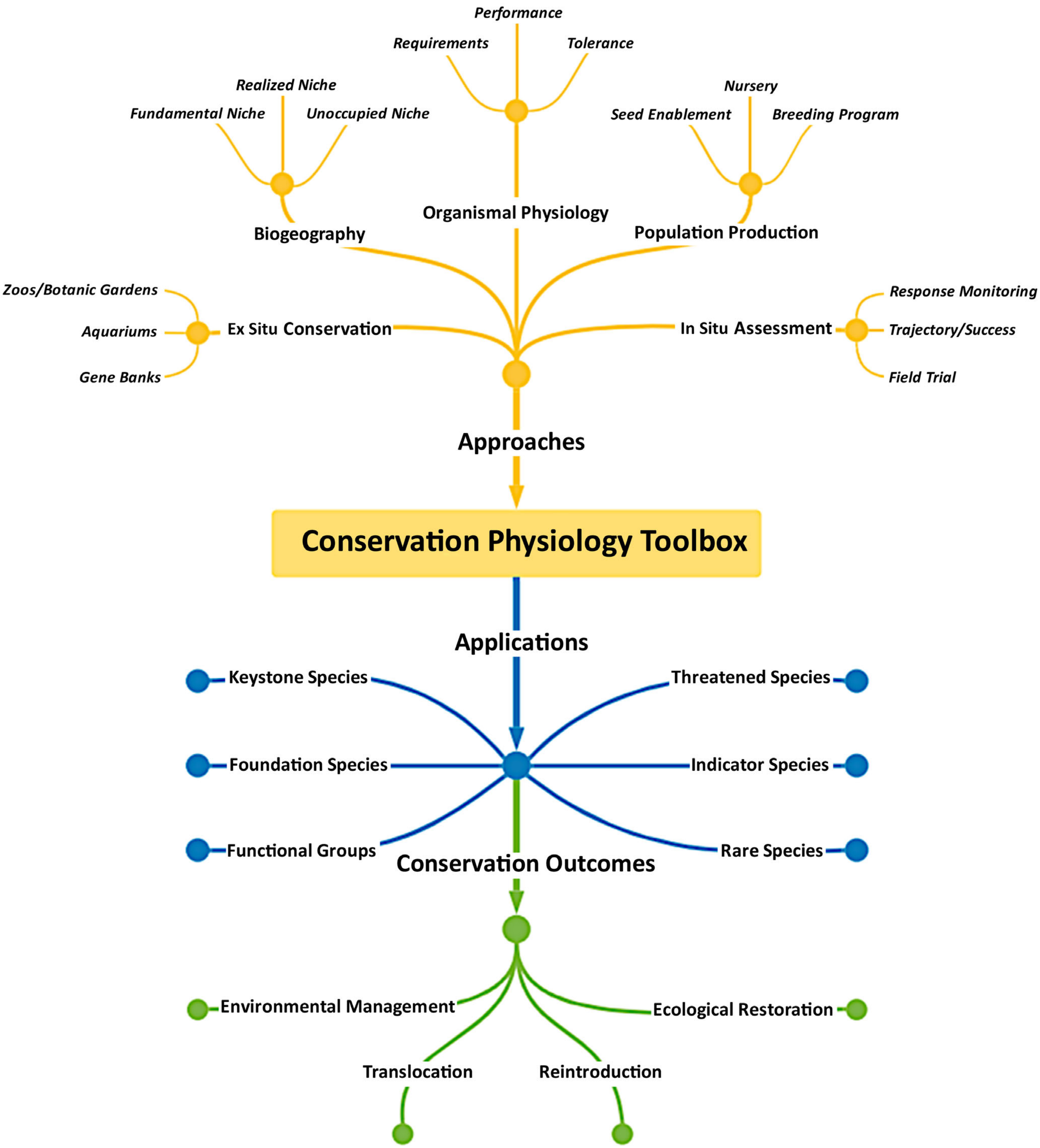

Figure 1. Schematic of a selection of research and analytical skills that contribute to the conservation physiology "toolbox" (yellow). Notably, this selection of methods, ranging from trait-oriented metrics, through performance metrics to endocrinology and biochemistry, is designed to express the breadth of techniques that can provide insight into environmental management. This selection is not exhaustive, nor are the six applications that we have identified (blue), all of which could be informed by any of the approaches that we have identified. We contend, however, that any combination of the physiological techniques and applications will advance the outcomes (green) of environmental management, translocation and reintroduction, ecological restoration, and ultimately biodiversity conservation.

restoration landscapes is central to reinstating self-sustaining ecosystems (Menz et al. 2011), but the landscapes being restored are typically more exposed, hotter, and drier than the predisturbance landscape (Tuff et al. 2016; Cross et al. 2020). Identifying thermal tolerance limits of ectotherms is a well-established process (Tomlinson 2019), but applying such approaches to provide practical guidance to ecological restoration programs requires fine-resolution spatial data to describing environmental, climatic, or edaphic factors to translate physiological performance to the "real world" (Tomlinson et al. 2017, 2019).

Where available, such data provide context for the physiological performance of focal species. Tomlinson et al. (2017) established the likely patterns of thermal bioenergetics of a suite of hymenopteran pollinators across a restoration landscape by integrating physiological performance with spatial data. Their models suggested that most key pollinators could tolerate the higher temperatures that characterized the restoration site, but that this increased their energetic requirements substantially. In revisiting the site, beetle pollinators were found to be highly thermally tolerant, and much more likely to provide pollination services across the landscape (Tomlinson 2020). While spatiotemporally specific, such findings highlight the importance of understanding ecosystem function and its many different parts. Increasing the availability of standardized geomorphology and edaphic datasets can make downscaling niche envelope models to project-level resolution an accessible and valuable management agenda. Adapting performance models to these outcomes can yield quantified estimates of the limitations and requirements of the focal taxa *in situ*, and potentially under changing climates, both of which we see as exciting and necessary future research directions for environmental management.

Assessing Requirements and Tolerances of Focal Taxa ("Organismal Physiology")

Developing models of complex species' requirements in niche space, such as those described earlier, requires direct measurements of their responses to stressors. Substantial insight can be gained by controlled, experimental studies (Cooke & Suski 2008), quantifying performance across a breadth of conditions. Better understanding the physiological constraints of key demographic life-stages or processes, can identify critical obstacles for the reinstatement of focal taxa to disturbed landscapes (James et al. 2013). For example, reinstating dominant *Triodia* grasslands has remained a significant challenge following mining activity, due to low and sporadic recruitment after disturbance (Erickson et al. 2017), despite the genus occurring across almost one third of the Australian arid zone where it is considered as a keystone species. The floral appendages (termed florets) encasing *Triodia* seeds significantly influence seed dormancy and tolerance to water stress, controlling seed germination against unpredictable periods (Lewandrowski et al. 2017*a*). Removing the florets imposed higher ecophysiological stress and mortality rates of >90% on emerging and establishing seedlings at temperatures >30°C (Lewandrowski et al. 2021). Under restoration scenarios, highly exposed surfaces can often be much hotter than those in natural ecosystems (Tuff et al. 2016), increasing recruitment challenges. Physiological insights that quantify the effects of hydrological regimes (e.g. Lewandrowski et al. 2017*b*; Rajapakshe et al. 2020), germination treatments (Erickson et al. 2017; Turner et al. 2018), soil amendments (Benigno et al. 2013; Bateman et al. 2019), or thermal tolerance and energetics (Tomlinson et al. 2015), have all proven effective in understanding how organisms respond to changed physical environments following mining, forestry and urban development. Furthermore, measuring physiological traits, such as those related to water status and use, can provide early insights into plant stress (Valliere et al. 2017, 2019). What we see as an important future avenue is the recognition of physiological performance in functional trait databases (e.g. Oliveira et al. 2017; Saatkamp et al. 2018; Kattge et al. 2020).

Optimizing *Ex Situ* Storage to Enhance Future Conservation and Restoration ("*Ex Situ* Conservation")

Ex situ storage vital to conservation is often facilitated through gene-banks, zoos, aquariums, and botanic gardens (Pritchard et al. 2012). To these ends, plant seeds can be used in many different ways including the production of conservation collections (Monks et al. 2019), as a repository of material for *in situ* conservation (Merritt & Dixon 2011; Pedrini et al. 2020), or to be held for future use in restoration (Turner this issue). Gene-banking like this can be a useful way to store material, but not all taxa respond well to storage conditions (Berjak & Pammenter 2013; Wyse & Dickie 2017). For conservation purposes, orthodox seeds are stored at low relative humidity (approximately 15–20%) and temperature (−18 to 15°C) to slow down all metabolic processes including dormancy loss and aging (Merritt & Dixon 2003). Where these conditions are inappropriate, cryogenic storage (in liquid nitrogen at −196°C) may be optimal for challenging or desiccation-sensitive germplasm such as zygotic embryos (extracted from recalcitrant seeds) and shoot tips in plants, and sperm, oocytes, and early stage embryos in animals for establishing critical *ex situ* base collections (Engelmann 2004; Pereira & Marques 2008). While technically challenging, valuable insights into the most appropriate methods for successful cryogenic storage of living tissues can be gained through analytical techniques such as differential scanning calorimetry that identify critical phase transitions and ice nucleation events (Nadarajan et al. 2008).

Nevertheless, even under ideal storage conditions orthodox seeds still age, albeit at a much slower rate, which can be rapidly quantified using artificial aging and comparative longevity measurements (Probert et al. 2009; Merritt et al. 2014) or more recently through metabolic assessment of seed quality (Dalziell & Tomlinson 2017). Determining species-specific responses during storage may guide management options such as follow-up seed collections, germination of material approaching longevity thresholds, or the use of more specialized storage environments for long-term storage for sensitive or conservation-dependent taxa (Hay & Probert 2013).

Storing genetic material for animal conservation remains in its infancy, and faces challenges in understanding what genetic and reproductive materials to collect and store (De Oliveira Silva et al. 2019), and how to extract and apply such resources for diverse wild species (Guy et al. 2020). Nevertheless, germplasm tissue banks for critically endangered animals exist at the Cincinnati and San Diego zoos (Loring 2016) and some conservation biologists already suggest de-extinction as the next ambitious target in reintroduction biology (Jørgensen 2013). Given the critical roles that some animals play in the provision of essential ecosystem services (i.e. pollination, seed dispersal, or predator control) and that they do not always return following ecological restoration (Cross et al. 2020), specifically reintroducing some critical fauna may be an important element of future restoration programs. To achieve such ambitions a greater understanding of the physiological responses of animal genetic material to genebanking is essential to more proactive management.

Producing Viable Populations for Reintroductions ("Population Production")

While the efforts of zoos and botanic gardens are critical in captive breeding and species reintroduction (Pritchard et al. 2012), many local enterprises can also apply conservation physiology to their own restoration nurseries. Assuming that viability has not been compromised by storage, seeds do not always germinate readily when needed, as dormancy may be present and acting as an obstacle to germination on demand (Pedrini & Dixon 2020). In most species where seed dormancy is present, combinations of abiotic conditions, such as moisture and incubation temperature, are critical to dormancy alleviation though the successful application of these factors varies immensely across species and seed dormancy classes (Kildisheva et al. 2020). Furthermore, stimuli such as ethylene, smoke, light, and nitrates may be required to initiate germination in quiescent, non-dormant seeds after (morpho)physiological seed dormancy has been alleviated (Merritt et al. 2007; Turner et al. 2018; Kildisheva et al. 2020). Seed physiological studies can be used to understand and define temperature and moisture limits for dormancy loss and germination using hydrothermal time models which can then be extrapolated over natural sites (Onofri et al. 2018; Rajapakshe this issue). Where disturbance takes place in landscapes with high biodiversity value, there is often a requirement to return populations of rare or threatened plants (Mcdonald et al. 2016). Detailed studies of threatened species have resulted in specific dormancy alleviation protocols for threatened plant species to develop *ex situ* collections for later reintroduction to post-mining restoration sites (Cochrane et al. 2007). As an example, detailed examination of the germination niche of one such species, *Ricinocarpos brevis* (Turner et al. 2018), improved the understanding of the drivers regulating both *ex situ* propagation and *in situ* recruitment with clear management implications.

Understanding how the germination niche can define patterns of ecology and endemism remains a developing field, especially in the context of physiological patterns and processes. For example, Rajapakshe et al. (2020) and Rajapakshe (this issue) recently explored the application of thermal performance breadth to understanding the germination niches of several closely related sympatric narrow range endemic and widely occurring species, finding that narrow range endemic species did not necessarily have the narrow germination niche that might be expected of them. Furthermore, the production of seed stocks suitable to reintroductions can be strongly influenced by the status of the maternal plant (Espeland & Hammond 2013). We suggest that physiological measurements of maternal plants, seeds, and seedlings could also provide insight into the importance of environmentally induced maternal effects during seed production for restoration.

Fauna reintroductions are most often used to create "insurance populations," but there is increasing evidence that not all species will return or interact with restoration in the manner that they use natural landscapes (Tomlinson et al. 2017; Cross et al. 2020). Both reproductive biology (Comizzoli & Holt 2019) and reintroduction biology (Armstrong & Seddon 2008) have strong conservation physiology components with which to produce viable reintroduction populations via captive breeding, and understanding the reproductive physiology and associated needs (e.g. specific resources) of focal species is valuable for their conservation (Tarszisz et al. 2014). Understanding the endocrine systems underpinning reproduction has the longest history in managing captive breeding populations (Mccormick & Romero 2017); yet despite this, many species of critical conservation value remain notoriously difficult to breed in captivity. As well, the captive breeding itself may produce stock that are not optimally suitable for release (Pritchard et al. 2012), partly due to a range of physiologically consequential stimuli that are only beginning to be considered, including unnatural photoperiods, and autoimmune considerations (Schulte-Hostedde & Mastromonaco 2015). As the number of species that require management and potential captive breeding increases, clearly engaging a broader range of physiological considerations to captive breeding programs will be beneficial.

Using Physiology to Inform Reintroduction Efforts ("*In Situ* Assessment")

Mechanistic monitoring, informed by physiological measurements, has long been understood to identify impediments to the success of translocation and reintroduction programs (Tarszisz et al. 2014). However, the capacity of such studies to suggest appropriate threat mitigation may be particularly important for narrow range taxa with specific habitat requirements, or in restoration contexts seeking to correct intensive disturbances following extractive industry. For example, combining hydrothermal germination requirements with targeted irrigation treatments (Lewandrowski et al. 2017*b*) that replicate natural rainfall patterns could help determine niche suitability, based on seed germination and seedling emergence as demographic filters. The ecological restoration of a site might be made more successful or more efficient by guiding irrigation rates with an understanding of the physiological requirements of the species being returned. Furthermore, production of reintroduction stock with appropriate adaptive capacity can be attained by selective breeding of genotypes with specific physiological traits, and can further be achieved by "hardening off" or stress-conditioning in the lead-up to release or out-planting, especially where key physiological constraints are understood (Valliere 2019; Valliere et al. 2019). Reconnection of degraded or disturbed communities with the surrounding undisturbed landscape can be enhanced by understanding physiological constraints to the return of key animal groups by planning targeted practices with understanding of energetic (Tomlinson et al. 2017; Tomlinson 2020), or thermal constraints of critical taxa (Cross et al. 2020). Once key physiological traits have been identified to guide management actions, the same traits can be used to monitor the trajectory and success of these efforts (Tarszisz et al. 2014; Valliere et al. 2021), potentially even providing insights into poor performance of target populations prior to their decline (Tarszisz et al. 2014; Valliere 2019).

Strategic Applications of Conservation Physiology in Ecological Restoration

While substantial detailed information can be accumulated by applying a comparative physiological paradigm to the interactions between an organism and its environment (Fisher & Owens 2004), there is a necessary trade-off between gathering the highly mechanistic, phylogenetically oriented understanding that eventuates from laboratory and short-term field studies, and biophysical modeling and the broader ecosystem function essential in successful ecological restoration (Young 2000; Miller et al. 2017). While such in-depth physiological understanding is not essential for all species or projects, throughout this article we have explored some key examples where these approaches provided insights into ecological restoration. To generalize such here, we have grouped some ecological roles together that are often traditionally considered separately because the consequences of understanding their physiology are conceptually similar. If a better understanding of the species' physiology facilitates their more rapid reinstatement in a restoration landscape, then the ecological roles that they play in the restructuring of the ecosystem will also be more rapidly and completely reinstated, and the consequences of this can cascade throughout the restoration ecosystem. Consequently, detailed physiological understanding can provide unique and useful insights for some crucially important groups, such as keystone species and foundation species, threatened species and rare species, indicator species, and critical functional groups that facilitate key ecological processes (Fig. 1).

Ecological Service Providers ("Functional Groups")

In every ecosystem there are some species that facilitate key ecosystem processes, such as nutrient cycling, predator–prey dynamics, or other key trophic interactions. Such taxa are the ecological service providers. Pollinators, particularly insects, have been the predominant focus of such conservation-oriented niche envelope models, including the example that we identified above describing the restoration of insect pollinator communities (Tomlinson et al. 2017; Tomlinson 2020). Few other taxa that provide key ecological services have, however, been subject to such attention, despite obvious insights to be gained in nutrient turnover (Pokhrel et al. 2021), or seed dispersal (Van Leeuwen et al. 2020), among others. In light of this, we argue that physiologically informed niche envelope models are currently an underutilized tool in environmental management, and specifically in ecological restoration.

Habitat preferences, behavior, and movement ecology of many key animal ecosystem service providers can be driven by their ecophysiological tolerances and requirements (Tuff et al. 2016; Garcia & Clusella-Trullas 2019; Cross et al. 2020). Some ecological services result as a cascade of movement ecology and physiology (Tarszisz et al. 2018). Some of these processes are essential in understanding how restored sites integrate with surrounding vegetation, and how the ecological processes that structure communities play out in a modified landscape, yet the physiological mechanisms driving these ecological processes are often poorly incorporated into restoration planning or monitoring (Cross et al. 2019). Understanding how changing patterns of animal movement interact with physiological processes has important management implications, especially in reconnecting restoration landscapes with relatively small patches, such as those resulting from mining and silviculture, with surrounding habitat.

Rare or Threatened Species ("Rare Species" and "Threatened Species")

For many rare and threatened species, critical baseline information about the species' ecology and physiology are often missing (Silcock et al. 2019). Furthermore, collecting these data, either under *ex situ* or *in situ* conditions, is constrained due to material scarcity, legislation, and accessibility to remote field sites (Monks et al. 2019). Biophysical ecology approaches have been used at large scales to understand likely refugia and physiological threats to threatened fauna, and even their assisted colonization (Mitchell et al. 2013), but it has always been challenging to interpret these at a practical scale (Tomlinson et al. 2017). However, when implemented at appropriate resolution, biophysical modeling can identify the most appropriate locations to focus monitoring efforts for threatened species (Porter et al. 2006), indicating a clear aspect where the conservation of rare animals can potentially be optimized in restoration and other managed landscapes by quantifying their specific requirements at a landscape level.

One of the greatest challenges to reintroduction success of threatened plants is water limitation, with a substantial number of trials receiving irrigation to improve survival (Silcock et al. 2019). Understanding species-specific water requirements or drought tolerance through targeted studies could be a valuable contribution to guiding rare and threatened species reintroduction, especially in restoration programs where the site has either been heavily degraded or completely altered and reconstructed. As noted earlier, the hydrothermal germination niche can be represented mathematically (Onofri et al. 2018; Rajapakshe this issue). Other germination traits such as germination rate, expressed as time to first germination, 10% germination, 50% germination, and maximum germination (Pedrini & Dixon 2020), can also determine the time required for suitable *in situ* conditions to support the early recruitment process. Understanding temporal windows may be particularly important for effective habitat matching for conservation-dependent taxa such as those found in specific environments or unusual substrates (Elliott et al. 2019). However, we also note that understanding the germination requirements of rare plants (e.g. Turner et al. 2013, 2018) is only the first step along the path to building biophysical models of plants that capture population demography in similar ways to those that exist for animals (Kearney & Porter 2017). We suggest that further key elements required might be understanding seedbank persistence and dynamics (i.e. dormancy cycling) and triggers to dormancy alleviation and germination promotion (Turner et al. 2013; Miller et al. 2019; Ooi 2019) and parameters related to maturation and reproductive phenology (Chia et al. 2015). Furthermore, germination is only a single demographic bottleneck in plant population ecology (James et al. 2013), and physiological parameterization of limitations in later life stages in plants (i.e. flower initiation, pollination, and seed development) will be equally important in predicting long-term survival and demographic trajectories.

Foundation and Keystone Species ("Foundation Species" and "Keystone Species")

Many ecosystems are defined by some species that are also potentially crucial in providing essential ecological conditions that profoundly influence the structure of the community. These are the foundation and keystone species, critical to ecosystems due to either their relative frequency (foundation species) or the key roles they fill in the community, disproportionate to their abundance (keystone species; Mills et al. 1993). There is a growing body of knowledge demonstrating ways to regenerate keystone species under both *ex situ* and *in situ* conditions (Erickson et al. 2017; Ensslin et al. 2018), and new technologies emerging to scale up and accelerate vegetation recovery processes (Erickson et al. 2017). However, such advances may be further optimized with physiological insights (James et al. 2013; Lewandrowski et al. 2017*b*). With appropriate consideration, foundation species' performance can be modeled to understand how appropriate material preparation can increase the likelihood of overcoming bottlenecks in recruitment success (Lewandrowski et al. 2017*b*, 2021). Although correlative distributional studies of keystone species are becoming more common in planning conservation (Dalmaris et al. 2015), we are unaware of any examples where such biophysical approaches have been applied to model the response of keystone species at landscape scales to guide ecological restoration. The difference between these approaches may seem subtle, but is important, and we envisage that such an exercise could provide interesting insights into where and when such species may face their greatest challenges. Physiological studies of foundation or keystone species could also provide mechanistic understanding of how these species influence other members of the communities (e.g. by microclimate amelioration, or the establishment of fertile islands). It is possible to develop appropriate representations of ecophysiological constraints for the species, so applying these at landscape scale is a clear extension of this work.

Indicator Species

Monitoring the restoration trajectory of a whole community, especially at large spatiotemporal scales, is one of the substantial challenges of ecological restoration (Miller et al. 2017). It is often most efficient to focus on a small suite of species in which changes of composition presage larger ecological shifts; these are indicator species (Ahmed et al. 2016). The challenge is identifying which species to monitor and few studies clearly justify these choices (Ahmed et al. 2016). Basing these selections on physiological metrics can provide empirical bases for this justification. In the example of restoring insect pollination explored earlier Tomlinson et al. (2017) suggested that the bee *Amegilla chlorocyanea* could be used as a baseline indicator because its energetic requirements far exceeded those of any other species in the hymenopteran pollination community. Alternatively, ant communities are often used as bioindicators to monitor the success of restoration in several ecosystems (Majer et al. 2013; Cross et al. 2016). Understanding the physiology of the ants involved provides insights into the mechanisms behind these ecological shifts, as habitat disturbance often promotes the abundance of thermophilic functional groups at the expense of more specialized functional groups that require a more varied thermal landscape (Hoffmann & Andersen 2003; Cross et al. 2016). Advances in understanding the physiology of such taxa could additionally advance ecological restoration.

The Challenges and Benefits to Incorporating Physiology into Ecological Restoration

A core element of the practical place of conservation physiology in ecological restoration is that a deep understanding of key species can have broad ecological consequences when it optimizes their return to a reassembling ecosystem. Understanding the physiological link between the organism and the environment, however, remains a dynamic field of study. The majority of studies define the environment in terms of climatic elements, principally temperature and water availability (Timlin et al. 2001; Tuff et al. 2016), and often consider them as univariate factors. There are, however, many other elements of the environment that define the niche, and which are substantially altered in landscapes requiring restoration, such as salinity, soil pH, and even wind dynamics (Biagi et al. 2019; Cross et al. 2021). Yet the physiological implications of such environmental change are poorly examined, and even where research has been devoted to the topic, the outcomes do not yet provide comprehensive understanding of the mechanisms and processes involved (Cross et al. 2021). Nor do we yet understand the physiological consequences of some ecological interactions. The example of insect pollinators examined here indicates the importance of simple ecological cascades of warmer microclimates imposing greater energetic requirements on insect pollinators that could be simply met by incorporating highly nectariferous plants into the understory restoration mix (Tomlinson et al. 2017). However, there are more intimate ecological interactions, particularly between plants and the soil microbial community, e.g. where the presence of some microbes substantially increases the performance of some plants in many different ways (Gellie et al. 2017; Baruch et al. 2020), yet the actual physiological pathways by which greater performance is achieved still provide substantial research opportunities. From a practical perspective, much of this research probably needs to be strongly established, since the application of microbial treatments to restoration sites is currently not considered best practice (Miller et al. 2017).

The associations between organisms and their environment tend to have a strong mechanistic basis when viewed through a physiological lens (Somero 2011), with the mechanisms underpinning ecological patterns easier to explain, predict, and therefore manage when examined this way. Despite this, the practical uptake of physiology is often limited (although for exceptions, see Valliere et al. 2021), with the persistent assumption that physiological assessments lack applicability at a practical scale (Cooke & Suski 2008; Tomlinson et al. 2014). Ecophysiological measurements are sometimes perceived as delivering abstract outcomes that are, at best, tangential to practical action (Cooke & Suski 2008). While it is true that many modern physiological measurements make use of very sophisticated and expensive tools (Cooke & Suski 2008), the long heritage of physiology as a discipline means that comparable measurements can be made using much simpler equipment and cost-effective approaches where necessary. Even a relatively superficial reflection can highlight the substantial practical insights and conservation outcomes to be gained by integrating a conservation physiology paradigm with targeted and meaningful applications (Fig. 1). However, it is necessary for conservation physiologists to engage further with the intellectual and practical challenges of environmental management and specifically, restoration ecology (Cooke & Suski 2008). Additionally, practitioners must collaborate with physiologists to facilitate bidirectional flows of knowledge to maximize the efficiency and success of conservation and restoration.

For more proactive stakeholders, the greater mechanistic understanding of the processes underpinning ecological restoration will be enough to encourage the uptake of physiology if it is made clear in the appropriate guidance statements and management frameworks (e.g. Valliere et al. 2021; Rajapakshe et al. this issue). Moreover, adaptive management holds a lot of promise for maximizing the practical applicability of physiology into conservation and restoration while minimizing long-term costs through evidence-based management actions. While Coristine et al. (2014) outline a conceptual framework for merging physiology with conservation, no systematic framework that we are aware of outlines how physiological approaches can be integrated across all stages of the adaptive management paradigm. This is beyond the scope of this article, though we believe such a framework is warranted.

Over a decade ago Cooke and Suski (2008) concluded that, in general, the integration of conservation physiology into ecological management and restoration had not been fully realized. While there have been advances in the way that ecophysiology is engaged with ecological restoration (e.g. Valliere et al. 2021), we are forced to conclude the same. We are not suggesting that conservation physiology is a panacea to address the challenges facing land-managers, simply that it has exceptional power to quantify the processes that structure ecosystem patterns and processes, and that this has not yet been employed to its fullest potential. Some key research questions have been suggested to bridge the gap between conservation physiology and environmental management, including ecological restoration and threatened species recovery (Cooke et al. 2021), and we have identified several more key avenues where conservation physiology can provide guidance and support, including applications to targeted focal groups, such as rare species, keystone species, and ecosystem service providers. Furthermore, integrating ecophysiological models with biogeographical data at high resolution allows specific planning of how these key focal groups may respond to ecological restoration and other management activity in space and time, providing a solid, and flexible paradigm that can incorporate diverse physiological measurements across taxa. Although these skills are specialized, a broader understanding of their value and potential by practitioners, policymakers, and regulators is essential in bridging the gap between knowledge and practice. However, we see promise emerging in the field of conservation physiology and a growing recognition of the challenge and complexity of practical applications by physiology researchers. Increasingly complex physiological concepts are being integrated across the range of restoration activities, from planning to monitoring and evaluation, and we expect this engagement to grow and expand across other environmental management initiatives. The encouragement of this growth is required to advance both conservation physiology and the success of management initiatives. Ultimately, we advocate strategic implementation of physiological measurements of this type, integrating conservation physiology at multiple scales to optimize efforts that restore or manage the environment, and ultimately to maximize biodiversity conservation outcomes.

Acknowledgment

This research was funded under the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (ICI150100041).

LITERATURE CITED

Ahmed AH, Siddig AA, Ellison AM, Ochs A, Villar-Leeman C, Lau MK (2016) How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecological Indicators 60:223–230. https://doi.org/10.1016/J.ECOLIND.2015.06.036

Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. Bioscience 61:782–789. https://doi.org/10.1525/bio.2011.61.10.8

Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. Trends in Ecology & Evolution 23:20–25. https://doi.org/10.1016/j.tree.2007.10.003

Baruch Z, Liddicoat C, Cando-Dumancela C, Laws M, Morelli H, Weinstein P, Young JM, Breed MF (2020) Increased plant species richness associates with greater soil bacterial diversity in urban green spaces. Environmental Research 196:110425. https://doi.org/10.1016/j.envres.2020.110425

Bateman AM, Erickson TE, Merritt DJ, Veneklaas EJ, Muñoz-Rojas M (2019) Water availability drives the effectiveness of inorganic amendments to increase plant growth and substrate quality. Catena 182:104116. https://doi.org/10.1016/j.catena.2019.104116

Beauregard F, De Blois S (2014) Beyond a climate-centric view of plant distribution: edaphic variables add value to distribution models. PLoS One 9: e92642. https://doi.org/10.1371/journal.pone.0092642

Benigno SM, Dixon KW, Stevens JC (2013) Increasing soil water retention with native-sourced mulch improves seedling establishment in postmine

Mediterranean sandy soils. Restoration Ecology 21:617–626. https://doi.org/10.1111/j.1526-100X.2012.00926.x

Berjak P, Pammenter N (2013) Implications of the lack of desiccation tolerance in recalcitrant seeds. Frontiers in Plant Science 4:478. https://doi.org/10.3389/fpls.2013.00478

Biagi KM, Oswald CJ, Nicholls EM, Carey SK (2019) Increases in salinity following a shift in hydrologic regime in a constructed wetland watershed in a post-mining oil sands landscape. Science of the Total Environment 653: 1445–1457. https://doi.org/10.1016/j.scitotenv.2018.10.341

Chia KA, Koch JM, Sadler R, Turner SR (2015) Developmental phenology of *Persoonia longifolia* (Proteaceae, R. Br) and the impact of fire on these events. Australian Journal of Botany 63:415–425. https://doi.org/10.1071/BT14315

Cochrane JA, Crawford AD, Monks LT (2007) The significance of *ex situ* seed conservation to reintroduction of threatened plants. Australian Journal of Botany 55:356–361. https://doi.org/10.1071/BT06173

Comizzoli P, Holt WV (2019) Breakthroughs and new horizons in reproductive biology of rare and endangered animal species. Biology of Reproduction 101:514–525. https://doi.org/10.1093/biolre/ioz031

Cooke SJ, Suski CD (2008) Ecological restoration and physiology: an overdue integration. Bioscience 58:957–968. https://doi.org/10.1641/B581009

Cooke SJ, Sack L, Franklin CE, Farrell AP, Beardall J, Wikelski M, Chown SL (2013) What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conservation Physiology 1:1–23. https://doi.org/10.1093/conphys/cot001

Cooke SJ, Bergmann JN, Madliger CL, Cramp RL, Beardall J, Burness G, et al. (2021) One hundred research questions in conservation physiology for generating actionable evidence to inform conservation policy and practice. Conservation Physiology 9:coab009. https://doi.org/10.1093/conphys/coab009

Coristine LE, Robillard CM, Kerr JT, O'connor CM, Lapointe D, Cooke SJ (2014) A conceptual framework for the emerging discipline of conservation physiology. Conservation Physiology 2:cou033. https://doi.org/10.1093/conphys/cou033

Cross SL, Cross AT, Merritt DJ, Dixon KW, Andersen AN (2016) Biodiversity responses to vegetation structure in a fragmented landscape: ant communities in a peri-urban coastal dune system. Journal of Insect Conservation 20: 485–495. https://doi.org/10.1007/s10841-016-9881-y

Cross SL, Tomlinson S, Craig MD, Dixon KW, Bateman PW (2019) Overlooked and undervalued: the neglected role of fauna and a global bias in ecological restoration assessments. Pacific Conservation Biology 25:331. https://doi.org/10.1071/PC18079

Cross S, Tomlinson S, Craig M, Bateman B (2020) The Time Local Convex Hull (T-LoCoH) method as a tool for assessing responses of fauna to habitat restoration: a case study using the perentie (*Varanus giganteus*: Reptilia: Varanidae). Australian Journal of Zoology 67:27–37. https://doi.org/10.1071/ZO19040

Cross AT, Stevens JC, Sadler R, Moreira-Grez B, Ivanov D, Zhong H, Dixon KW, Lambers H (2021) Compromised root development constrains the establishment potential of native plants in unamended alkaline post-mining substrates. Plant and Soil 46:163–179. https://doi.org/10.1007/s11104-018-3876-2

Dalmaris E, Ramalho CE, Poot P, Veneklaas EJ, Byrne M (2015) A climate change context for the decline of a foundation tree species in south-western Australia: insights from phylogeography and species distribution modelling. Annals of Botany 116:941–952. https://doi.org/10.1093/aob/mcv044

Dalziell EL, Tomlinson S (2017) Reduced metabolic rate indicates declining viability in seed collections: an experimental proof-of-concept. Conservation Physiology 5:cox058. https://doi.org/10.1093/conphys/cox058

De Oliveira Silva R, Ahmadi BV, Hiemstra SJ, Moran D (2019) Optimizing *ex situ* genetic resource collections for European livestock conservation. Journal of Animal Breeding and Genetics 136:63–73. https://doi.org/10.1111/jbg.12368

Ehleringer JR, Sandquist DR (2006) Ecophysiological constraints on plant responses in a restoration setting. Pages 42–58. In: Falk DA, Palmer MA, Zedler JB (eds) Foundations of restoration ecology. Island Press, Washington D.C.

Elliott CP, Lewandrowski W, Miller BP, Barrett M, Turner S (2019) Identifying germination opportunities for threatened plant species in episodic ecosystems by linking germination profiles with historic rainfall events. Australian Journal of Botany 67:256–267. https://doi.org/10.1071/BT18215

Engelmann F (2004) Plant cryopreservation: progress and prospects. In Vitro Cellular & Developmental Biology - Plant 40:427–433. https://doi.org/10.1079/IVP2004541

Ensslin A, Van De Vyver A, Vanderborght T, Godefroid S (2018) *Ex situ* cultivation entails high risk of seed dormancy loss on short-lived wild plant species. Journal of Applied Ecology 55:1145–1154. https://doi.org/10.1111/1365-2664.13057

Erickson TE, Muñoz-Rojas M, Kildisheva OA, Stokes BA, White SA, Heyes JL, et al. (2017) Benefits of adopting seed-based technologies for rehabilitation in the mining sector: a Pilbara perspective. Australian Journal of Botany 65: 646–660. https://doi.org/10.1071/BT17154

Espeland EK, Hammond D (2013) Maternal effects on growth and competitive ability in a commonly used restoration species. Native Plants Journal 14: 231–242. https://doi.org/10.3368/npj.14.3.231

Fisher DO, Owens IP (2004) The comparative method in conservation biology. Trends in Ecology & Evolution 19:391–398. https://doi.org/10.1016/j.tree.2004.05.004

Garcia RA, Clusella-Trullas S (2019) Thermal landscape change as a driver of ectotherm responses to plant invasions. Proceedings of the Royal Society B 286:20191020. https://doi.org/10.1098/rspb.2019.1020

Gellie NJ, Mills JG, Breed MF, Lowe AJ (2017) Revegetation rewilds the soil bacterial microbiome of an old field. Molecular Ecology 26:2895–2904. https://doi.org/10.1111/mec.14081

Guy EL, Gillis AB, Kouba AJ, Barber D, Poole V, Marcec-Greaves RM, Kouba CK (2020) Sperm collection and cryopreservation for threatened newt species. Cryobiology 94:80–88. https://doi.org/10.1016/j.cryobiol.2020.04.005

Hale SL, Koprowski JL (2018) Ecosystem-level effects of keystone species reintroduction: a literature review. Restoration Ecology 26:439–445. https://doi.org/10.1111/rec.12684

Hay FR, Probert RJ (2013) Advances in seed conservation of wild plant species: a review of recent research. Conservation Physiology 1:cot030. https://doi.org/10.1093/conphys/cot030

Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology 28:444–464. https://doi.org/10.1046/j.1442-9993.2003.01301.x

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427. https://doi.org/10.1101/SQB.1957.022.01.039

James JJ, Sheley RL, Erickson T, Rollins KS, Taylor MH, Dixon KW (2013) A systems approach to restoring degraded drylands. Journal of Applied Ecology 50:730–739. https://doi.org/10.1111/1365-2664.12090

Jørgensen D (2013) Reintroduction and de-extinction. Bioscience 63:719–720. https://doi.org/10.1093/bioscience/63.9.719

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, et al. (2020) TRY plant trait database–enhanced coverage and open access. Global Change Biology 26:119–188. https://doi.org/10.1111/gcb.14904

Kearney MR, Porter WP (2017) NicheMapR-an R package for biophysical modelling: the microclimate model. Ecography. 40:664–674. https://doi.org/10.1111/ecog.02360

Kildisheva OA, Dixon KW, Silveira FA, Chapman T, Di Sacco A, Mondoni A, Turner SR, Cross AT (2020) Dormancy and germination: making every seed count in restoration. Restoration Ecology 28:S256–S265. https://doi.org/10.1111/rec.13140

Lannuzel G, Balmot J, Dubos N, Thibault M, Fogliani B (2021) High-resolution topographic variables accurately predict the distribution of rare plant species for conservation area selection in a narrow-endemism hotspot in New Caledonia. Biodiversity and Conservation 30:963–990. https://doi.org/10.1007/s10531-021-02126-6

Lewandrowski W, Erickson TE, Dalziell EL, Stevens JC (2017a) Ecological niche and bet-hedging strategies for Triodia (R. Br.) seed germination. Annals of Botany 121:367–375. https://doi.org/10.1093/aob/mcx158

Lewandrowski W, Erickson TE, Dixon KW, Stevens JC (2017b) Increasing the germination envelope under water stress improves seedling emergence in two dominant grass species across different pulse rainfall events. Journal of Applied Ecology 54:997–1007. https://doi.org/10.1111/1365-2664.12816

Lewandrowski W, Stevens JC, Webber BL, Dalziell EL, Trudgen MS, Bateman AM, Erickson TE (2021) Global change impacts on arid zone ecosystems: seedling establishment processes are threatened by temperature and water stress. Ecology and Evolution 11:8071–8084. https://doi.org/10.1002/ece3.7638

Loring JF (2016) Stem cells and the frozen zoo. Genetic Engineering & Biotechnology News 36:36–37. https://doi.org/10.1089/gen.36.14.16

MacMahon JA, Holl KD (2001) Ecological restoration: a key to conservation biology's future. Pages 245–269. In: Soulé ME, Orians G (eds) Research priorities in conservation biology. Island Press, Washington D.C.

Majer JD, Heterick B, Gohr T, Hughes E, Mounsher L, Grigg A (2013) Is thirty-seven years sufficient for full return of the ant biota following restoration? Ecological Processes 2:1–12. https://doi.org/10.1186/2192-1709-2-19

Mccormick SD, Romero LM (2017) Conservation endocrinology. Bioscience 67: 429–442. https://doi.org/10.1093/biosci/bix026

Mcdonald T, Gann GD, Jonson J, Dixon KW (2016) International standards for the practice of ecological restoration—including principles and key concepts. Society for Ecological Restoration, Washington D.C.

Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science 16:4–12. https://doi.org/10.1016/j.tplants.2010.09.006

Merritt DJ, Dixon KW (2003) Seed storage characteristics and dormancy of Australian indigenous plant species: from the seed store to the field. Pages 807–823. In: Smith D, Dickie JB, Linington SH, Pritchard HW, Probert RJ (eds) Seed conservation: turning science into practice. The Royal Botanic Gardens, Kew, London, United Kingdom

Merritt DJ, Dixon KW (2011) Restoration seed banks—a matter of scale. Science 332:424–425. https://doi.org/10.1126/science.1203083

Merritt DJ, Turner SR, Clarke S, Dixon KW (2007) Seed dormancy and germination stimulation syndromes for Australian temperate species. Australian Journal of Botany 55:336–344. https://doi.org/10.1071/BT06106

Merritt D, Martyn A, Ainsley P, Young R, Seed L, Thorpe M, et al. (2014) A continental-scale study of seed lifespan in experimental storage examining seed, plant, and environmental traits associated with longevity. Biodiversity and Conservation 23:1081–1104. https://doi.org/10.1007/s10531-014-0641-6

Miller BP, Sinclair EA, Menz MHM, Elliott CP, Bunn E, Commander LE, et al. (2017) A framework for the practical science necessary to restore sustainable, resilient and biodiverse ecosystems. Restoration Ecology 25: 605–617. https://doi.org/10.1111/rec.12475

Miller BP, Symonds D, Barrett M (2019) Persistence of rare species depends on rare events: demography, fire response and phenology of two plant species endemic to a semi-arid Banded Iron Formation range. Australian Journal of Botany 67:268–280. https://doi.org/10.1071/BT18214

Mills L, Soulé M, Doak D (1993) The keystone-species concept in ecology and conservation. Bioscience 43:219–224. https://doi.org/10.2307/1312122

Mitchell N, Hipsey M, Arnall S, Mcgrath G, Bin Tareque H, Kuchling G, Vogwill R, Sivapalan M, Porter W, Kearney M (2013) Linking eco-energetics and eco-hydrology to select sites for the assisted colonization of Australia's rarest reptile. Biology 2:1–25. https://doi.org/10.3390/biology2010001

Monks L, Barrett S, Beecham B, Byrne M, Chant A, Coates D, Cochrane JA, Crawford A, Dillon R, Yates C (2019) Recovery of threatened plant species and their habitats in the biodiversity hotspot of the Southwest Australian Floristic Region. Plant Diversity 41:59–74. https://doi.org/10.1016/j.pld.2018.09.006

Nadarajan J, Marzalina M, Krishnapillay B, Staines HJ, Benson EE, Harding K (2008) Application of differential scanning calorimetry in developing cryopreservation strategies for *Parkia speciosa*, a tropical tree producing recalcitrant seeds. CryoLetters 29:95–110

Oliveira BF, São-Pedro VA, Santos-Barrera G, Penone C, Costa GC (2017) AmphiBIO, a global database for amphibian ecological traits. Scientific Data 4:1–7. https://doi.org/10.1038/sdata.2017.123

Onofri A, Benincasa P, Mesgaran MB, Ritz C (2018) Hydrothermal-time-to-event models for seed germination. European Journal of Agronomy 101: 129–139. https://doi.org/10.1016/j.eja.2018.08.011

Ooi MK (2019) The importance of fire season when managing threatened plant species: a long-term case-study of a rare *Leucopogon* species (Ericaceae). Journal of Environmental Management 236:17–24. https://doi.org/10.1016/j.jenvman.2019.01.083

Pedrini S, Dixon KW (2020) International principles and standards for native seeds in ecological restoration. Restoration Ecology 28:S286–S303. https://doi.org/10.1111/rec.13155

Pedrini S, Gibson-Roy P, Trivedi C, Gálvez-Ramírez C, Hardwick K, Shaw N, Frischie S, Laverack G, Dixon K (2020) Collection and production of native seeds for ecological restoration. Restoration Ecology 28: S228–S238. https://doi.org/10.1111/rec.13190

Pereira RM, Marques CC (2008) Animal oocyte and embryo cryopreservation. Cell and Tissue Banking 9:267–277. https://doi.org/10.1007/s10561-008-9075-2

Pokhrel MR, Cairns SC, Hemmings Z, Floate KD, Andrew NR (2021) A review of dung beetle introductions in the Antipodes and North America: status, opportunities, and challenges. Environmental Entomology 50:762–780. https://doi.org/10.1093/ee/nvab025

Porter WP, Vakharia N, Klousie WD, Duffy D (2006) Po'ouli landscape bioinformatics models predict energetics, behavior, diets, and distribution on Maui. Integrative and Comparative Biology 46:1143–1158. https://doi.org/10.1093/icb/icl051

Pritchard DJ, Fa JE, Oldfield S, Harrop SR (2012) Bring the captive closer to the wild: redefining the role of *ex situ* conservation. Oryx 46:18–23. https://doi.org/10.1017/S0030605310001766

Probert RJ, Daws MI, Hay FR (2009) Ecological correlates of *ex situ* seed longevity: a comparative study on 195 species. Annals of Botany 104:57–69. https://doi.org/10.1093/aob/mcp082

Rajapakshe PVGSWR, Turner SR, Cross AT, Tomlinson S (2020) Hydrological and thermal responses of seeds from four co-occurring tree species from southwest Western Australia. Conservation Physiology 8:coaa021. https://doi.org/10.1093/conphys/coaa021

Saatkamp A, Cochrane A, Commander L, Guja LK, Jimenez-Alfaro B, Larson J, et al. (2018) A research agenda for seed-trait functional ecology. New Phytologist 221:1764–1775. https://doi.org/10.1111/nph.15502

Schulte-Hostedde AI, Mastromonaco GF (2015) Integrating evolution in the management of captive zoo populations. Evolutionary Applications 8: 413–422. https://doi.org/10.1111/eva.12258

Silcock JL, Simmons CL, Monks L, Dillon R, Reiter N, Jusaitis M, Vesk PA, Byrne M, Coates DJ (2019) Threatened plant translocation in Australia: a review. Biological Conservation 236:211–222. https://doi.org/10.1016/j.biocon.2019.05.002

Somero GN (2011) Comparative physiology: a "crystal ball" for predicting consequences of global change. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 301:R1–R14. https://doi.org/10.1152/ajpregu.00719.2010

Tarszisz E, Dickman CR, Munn AJ (2014) Physiology in conservation translocations. Conservation Physiology 2:cou054. https://doi.org/10.1093/conphys/cou054

Tarszisz E, Tomlinson S, Harrison ME, Morrough-Bernard HC, Munn AJ (2018) An ecophysiologically-informed model of seed dispersal by orangutans: linking animal movement with gut passage across time and space. Conservation Physiology 6:coy013. https://doi.org/10.1093/conphys/coy013

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C (2017) Future threats to biodiversity and pathways to their prevention. Nature 546:73–81. https://doi.org/10.1038/nature22900

Timlin D, Pachepsky Y, Walthall C, Loechel S (2001) The use of a water budget model and yield maps to characterize water availability in a landscape. Soil and Tillage Research 58:219–231. https://doi.org/10.1016/S0167-1987(00)00170-7

Tomlinson S (2019) The mathematics of thermal sub-optimality: nonlinear regression approaches to thermal performance in reptile metabolic rates. Journal of Thermal Biology 81:49–58. https://doi.org/10.1016/j.jtherbio.2019.02.008

Tomlinson S (2020) The construction of small-scale, quasi-mechanistic spatial models of insect energetics in habitat restoration: a case study of beetles in Western Australia. Diversity and Distributions 26:1016–1033. https://doi.org/10.1111/ddi.13074

Tomlinson S, Arnall S, Munn AJ, Bradshaw SD, Maloney SK, Dixon KW, Didham RK (2014) Applications and implications of ecological energetics. Trends in Ecology & Evolution 29:280–290. https://doi.org/10.1016/j.tree.2014.03.003

Tomlinson S, Dixon KW, Didham RK, Bradshaw SD (2015) Physiological plasticity of metabolic rates in the invasive honey bee and an endemic Australian bee species. Journal of Comparative Physiology B 8:835–844. https://doi.org/10.1007/s00360-015-0930-8

Tomlinson S, Webber BL, Bradshaw SD, Dixon KW, Renton M (2017) Incorporating biophysical ecology into high-resolution restoration targets: insect pollinator habitat suitability models. Restoration Ecology 26:338–347. https://doi.org/10.1111/rec.12561

Tomlinson S, Lewandrowski W, Elliott CP, Miller BP, Turner SR (2019) High resolution distribution modelling of a threatened short-range endemic plant informed by edaphic factors. Ecology and Evolution 10:763–777. https://doi.org/10.1002/ece3.5933

Tuff KT, Tuff T, Davies KF (2016) A framework for integrating thermal biology into fragmentation research. Ecology Letters 19:361–374. https://doi.org/10.1111/ele.12579

Turner S, Best C, Barrett S (2013) Combining science with management: understanding the seed ecology of "pearl-like Androcalva" underpins successful *in situ* regeneration by fire of this threatened species. Australasian Ecology 22:19–21

Turner SR, Lewandrowski W, Elliott CP, Merino-Martín L, Miller BP, Stevens JC, Erickson TE, Merritt DJ (2018) Seed ecology informs restoration approaches for threatened species in water-limited environments: a case study on the short-range Banded Ironstone endemic *Ricinocarpos brevis* (Euphorbiaceae). Australian Journal of Botany 65:661–677. https://doi.org/10.1071/BT17155

Valliere JM (2019) Effects of defoliation and herbivore exclosures on growth and reproduction of transplanted bunchgrass seedlings. Ecological Restoration 37:213–217. https://doi.org/10.3368/er.37.4.213

Valliere JM, Irvine IC, Santiago L, Allen EB (2017) High N, dry: experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought. Global Change Biology 23:4333–4345. https://doi.org/10.1111/gcb.13694

Valliere JM, Zhang J, Sharifi MR, Rundel PW (2019) Can we condition native plants to increase drought tolerance and improve restoration success? Ecological Applications 29:e01863. https://doi.org/10.1002/eap.1863

Valliere JM, Ruscalleda Alvarez J, Cross AT, Lewandrowski W, Riviera F, Stevens JC, et al. (2021) Restoration ecophysiology: an ecophysiological approach to improve restoration strategies and outcomes in severely disturbed landscapes. Restoration Ecology. https://doi.org/10.1111/rec.13571

Van Leeuwen CH, Tella JL, Green AJ (2020) Animal-mediated dispersal in understudied systems. Frontiers in Ecology and Evolution 7:508. https://doi.org/10.3389/fevo.2019.00508

Volis S (2019) Conservation-oriented restoration—a two for one method to restore both threatened species and their habitats. Plant Diversity 41:50–58. https://doi.org/10.1016/j.pld.2019.01.002

White L, Catterall C, Tomlinson S, Taffs K (2020) Rare or overlooked? The distribution of Hairy Jointgrass in north coast New South Wales, Australia, and implications for its conservation status. Journal of Nature Conservation 54:125792. https://doi.org/10.1016/j.jnc.2020.125792

Wikelski M, Cooke SJ (2006) Conservation physiology. Trends in Ecology & Evolution 21:38–46. https://doi.org/10.1016/j.tree.2005.10.018

Wyse SV, Dickie JB (2017) Predicting the global incidence of seed desiccation sensitivity. Journal of Ecology 105:1082–1093. https://doi.org/10.1111/1365-2745.12725

Young TP (2000) Restoration ecology and conservation biology. Biological Conservation 92:73–83. https://doi.org/10.1016/S0006-3207(99)00057-9

Zurell D, König C, Malchow AK, Kapitza S, Bocedi G, Travis J, Fandos G (2021) Spatially explicit models for decision-making in animal conservation and restoration. Ecography. https://doi.org/10.1111/ecog.05787

Coordinating Editor: Jeremy James

Received: 18 July, 2021; First decision: 14 September, 2021; Revised: 7 December, 2021; Accepted: 10 December, 2021