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PERSPECTIVES AND PARADIGMS

Improving science-based invasive species management with physiological knowledge, concepts, and tools

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Abstract Biological invasions are a prominent factor contributing to global biodiversity loss. As a result, managing invasive species is a priority for many conservation scientists and natural resource managers. Invasive species management requires a multidisciplinary approach and there is increasing recognition that physiology can be used to inform conservation efforts because physiological processes underlie an individual's response to its environment. For example, physiological concepts and tools can be used to assess the impacts of invasive animals on their new ecosystems, to predict which animal species are likely to become invasive, to prevent the introduction of non-native animals, and to control incipient or established invasions. To evaluate whether physiology is integrated within invasion science, the journal *Biological Invasions* was surveyed for a quantitative literature review. To determine how physiology is used to inform invasion science and which subdisciplines of physiology are particularly relevant to invasive animal management, the broader invasion literature was also reviewed to identify examples where physiology has contributed to studying and managing invasive animals. Only 6 % of articles published in *Biological Invasions* incorporated physiological knowledge or tools, mostly for the purposes of identifying traits associated with species invasiveness (i.e. prediction). However, the broader literature indicated that successful invasive species research and management can be supported by fundamental and applied physiological research for assessing, predicting, preventing, and controlling invasive animals. Development of new techniques and increased availability of equipment for remote or rapid monitoring of physiology in the field will increase opportunities for integrating physiology within invasion science.

Keywords Conservation physiology · Invasive species · Invasion management · Macrophysiology

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Introduction

Invasive plants, animals, and microbes have become established in many terrestrial, marine, and freshwater ecosystems (Williamson 1998; Parker et al. 1999). These biological invasions are important agents of global biodiversity homogenization, habitat alteration, and species extirpation (Gurevitch and Padilla 2004).

Most instances in which a non-native species is introduced into a new habitat are facilitated by humans (Baskin 1996) because global trade and world travel have multiplied the vectors available for introducing non-native species (Carlton 1987; Bright 1999; Perrings et al. 2005; Simberloff et al. 2005; Meyerson and Mooney 2007). However, fewer than 10 % of introduced species (i.e. potential invaders) cause significant impacts (Williamson and Fitter 1996) because many fail to establish in their new range due to biotic or abiotic constraints. Minimally, invasive species must be physiologically capable of persisting in their new environment to survive, reproduce successfully, expand their range, and ultimately establish as invasive (Williamson 1996; Kolar and Lodge 2001; Blackburn et al. 2011). However, not all introduced species are liable to become invasive and physiological characteristics can contribute to invasiveness (e.g. Kelley 2014).

Invasion science broadly focuses on either assessment of impacts that invasive species have on local ecosystems or directly on the management of invasive species, which includes predicting which species are likely to become invasive, preventing the introduction of invasive species, and controlling established or incipient invasions. Invasion science is necessarily complex and multidisciplinary (Leung et al. 2002) and requires consideration of many processes including behavior (Holway and Suarez 1999), ecology (Peterson 2003), genetics (Lee 2002; Prentis and Pavasovic 2013), and economics (Leung et al. 2002). Physiology has the potential to be equally important and has received increasing attention as a domain with the capacity to contribute to conservation science and natural resource management (Wikelski and Cooke 2006; Cooke et al. 2013) because physiology is the internal mechanism that regulates an animal's response to its environment. In any situation where an organism is challenged or confronted with change, physiological responses are responsible for determining the course of action taken for maintaining homeostasis. Physiology can therefore provide relevant information when considering biological invasions (Cooke et al. 2013).

Given that funding can be a limiting factor when developing environmental remediation or conservation efforts (Brown and Shogren 1998), it is essential that strategies chosen for environmental management are efficient (Sutherland et al. 2004). Consideration of physiological processes and utilization of physiological tools have the potential to be important components of the invasion science toolbox because they can facilitate rapid assessment of individuals and lead to decisive action. To evaluate whether physiology is integrated with invasion research and management, a quantitative literature survey was conducted of the journal *Biological Invasions*, followed by a broader literature review to determine how physiology is used in the context of invasion science; the search focused on determining which research and management objectives rely on physiological methods and knowledge as well as identifying which subdisciplines of physiology are relevant. Throughout, we focus on four key objectives of invasion science and discuss physiology in the context of those objectives: assessing the impact of invasions, predicting the identity of potential invasive species, preventing invasions, and controlling invasive species that have been introduced (i.e. incipient invasions) or become established in a new range. The scope of this paper is limited to invasive animals, although many of the principles are applicable to the management of invasive plant species.

Approach

To evaluate the extent to which physiology is presently integrated within invasion science, a bibliometric analysis of the prominent invasive species journal *Biological Invasions* was conducted. Original research articles published in *Biological Invasions* were sorted through the Scopus search engine to identify those that incorporated physiological tools or considered physiological processes, consistent with the definition of conservation physiology established in Cooke et al. (2013). Papers were filtered to include only articles published between 1999 (year of the journal's inception) and 2013. The resulting 1737 articles were manually screened by reviewing the abstract. After downloading relevant articles, they were categorized based on the physiological tools that they implemented as well as the invasive species research or management objective of the study in order to determine the relative importance of different physiological subdisciplines and provide a foundation for identifying physiological tools that could be better developed.

To expand on the findings beyond our search of *Biological Invasions* publications, a broader literature search was conducted to identify how physiology has been incorporated for the assessment, prediction, prevention, and control of invasive species and to determine which physiological subdisciplines are relevant to these research and management objectives. These findings are used to identify past successes of physiology in informing invasion science, support the development of a framework for incorporating physiology within invasion science, and identify areas in which different physiological subdisciplines are potentially relevant to invasion science (Cooke et al. 2013; Table 1). Although additional papers are not included in the bibliometric analysis (which is meant to be informative rather than exhaustive because it is based solely on publications in *Biological Invasions*), they are used to support the conclusions and provide concrete examples of the synergy between physiology and invasion science. Graphics were generated using ggplot2 in R (R Core Team 2014).

Findings

Is physiology integrated within invasion science?

Among 1737 articles published in *Biological Invasions*, 105 (6 %), incorporated physiology and were therefore pertinent to the research aims. In the past nine years there appears to be growing integration with physiology, with increasing proportions of relevant publications in *Biological Invasions* between 2005 and 2013 (Fig. 1). However, integration was highest in the years 2003 and 2004. The 105 research articles implemented a variety of physiological tools for studying invasions but predominantly focused on ecophysiology and various aspects of energetics of introduced species (Fig. 2). When categorizing the studies by research objective, most studies integrated physiology when describing or explaining invasions, which was sorted into a category with predicting invasions (73 %) given that the most closely related management objective that could be derived from this would be using the information to forecast whether the species would invade elsewhere or to identify traits that facilitate invasion. Indeed, using such information can be useful for predicting invasions, which is an important proactive approach to invasive species management (Box 1) and many of the articles explicitly acknowledged the usefulness of identifying traits that may predict invasiveness even when that was not necessarily the direct objective of that article. Overall, few studies used physiology for the purposes of assessing impacts of native species (15 %), preventing invasions (4 %), or controlling invasions (8 %). Most of the articles focused on animals (53 %), with most animal studies concentrating on invertebrate (66 %) rather than vertebrate species. Among invertebrates, articles studied primarily invasive arthropods (e.g. crabs, crayfish, and insects) or invasive molluscs (e.g. snails and mussels). Most vertebrate studies focused on fish, but there were also examples of invasive turtles, frogs, birds, and one instance of an invasive mammal.

How is physiology used within the context of invasion science?

Assessing biological impacts of invasive species

Given the ecological and economic consequences of biological invasions, considerable research has been conducted to evaluate the impacts of non-native species and to study the effects of invasions on native biota and landscapes. Physiological tools can be used for evaluating the impacts of invasive animals on native species and ecosystems, for example by measuring the effects of interactions on fitness from a subset of the population. Ecological metrics, such as population declines of native species, are not always evident or easy to measure early in an invasion process. Alternatively, physiological metrics such as stress physiology can be analyzed quickly and sometimes remotely to measure sublethal responses of native species to the presence of introduced or invasive species (Cooke et al. 2013).

Physiological changes can index the stress response of animals and provide information about impacts of invasions on ecosystems. Living in the presence of invasive species can result in a stress response, including the secretion of stress hormones (i.e. glucocorticoids, catecholamines) into circulation, chronic elevation of which can result in increased heart rate, higher energetic demand, as well as behavioural changes and tertiary stress responses (Barton 2002) including challenges to metabolism, growth, and reproduction (Wikelski and Cooke 2006). These may be evident when native species face competition from invasive species or simply in the presence of invasive

Table 1 A summary of physiological disciplines that contribute to the study or management of biological invasions. Physiological subdisciplines are adapted from Cooke et al. (2013)

Discipline	Application within invasive species research	Select citations
Bioenergetics and Nutrition	• Measure nutrient cycling by invasive species to assess impacts on its new habitat	Liss et al. (2013)
	• Bioenergetic and nutritional constraints approximate the energetic and metabolic costs associated with introduction to a new habitat and can be used to predict the invasive range of non-native species	Goedkoop et al. (2011)
Cardiorespiratory physiology	• Remote monitoring of heart rate can provide information about the stress of species, which could be related to their invasiveness or interactions with native and invasive species (e.g. via remote biologging)	Iftikar et al. (2014)
	• Identification of the upper thermal temperature threshold and heart rate failure temperature of potential competitors can be used to determine the invasiveness of a non-native species	
Comparative physiology	• Comparative physiology can provide insight into the mechanisms that drive invasiveness and therefore be used to predict invasions	Somero (2011)
	• Comparing physiology of similar species can provide a proximate estimate for physiological sensitivity to the environment or to certain toxins	
Endocrinology	• Reproductive hormones can be used to monitor the reproductive status of invasive species to determine whether it is likely to become invasive	Moore et al. (2005)
	• Hormone titres show sub-lethal consequences of invasions and can be used to determine which species are negatively affected by an invasive species	Graham et al. (2012)
	• Successful invasive species are often characterized by attenuated stress responses, knowledge that can be used for identifying potentially invasive species	Liebl and Martin (2012)
Ecophysiology	• Evaluating tolerance of a non-native species to abiotic conditions such as temperature or salinity can be used to predict whether an animal is physiologically capable of surviving in the novel environment and becoming invasive	Kearney and Porter (2009) Rödder et al. (2009)
	• Species distribution models that incorporate ecophysiological traits of potentially invasive species tend to perform better than models that rely on species' natural history	
Evolutionary physiology	• Measures adaptability to new biotic and abiotic environments and modify their diet, or adapt to toxins	McKenzie et al. (2011)
Genomics	• Genomics can identify gene expression mechanisms for acclimatizing to novel habitats	Lee (2002)
	• Genome sequencing can allow development of double-stranded RNA for species-specific control	Lockwood et al. (2010)
Immunology	• Immunological profiles can be used to predict whether a species will become invasive	Lee and Klasing (2004)
	• Identification of the effects of biological control agents on native and invasive species prior to implementation.	
Locomotor physiology	• Degree of locomotor performance determines the ability of a species to spread across a landscape	Phillips et al. (2006), Lee et al. (2013)
	• Locomotor performance can influence the effectiveness of barriers	
Reproductive physiology	• Immunocontraception is a field with potential for reducing the spread of invaders	Kirkpatrick et al. (2011)
Sensory physiology	• Create a non-physical barrier that inhibits the ability of a species to spread across a landscape	Wagner et al. (2006)
	• Exploiting various sensory mechanisms of target species to influence the direction of movement and coerce animals into traps	
Toxicology	• Identification of conflicts between toxic invaders and native species	Lapidge et al. (2007)
	• Lethal control with poisonous chemicals	

species. Graham et al. (2012) found that native fence lizards (*Sceloporus undulatus*) living in areas with invasive fire ants (*Solenopsis invicta*) had higher baseline and acute circulating cortisol relative to lizards living in fire ant free territories. Living under stress increases metabolic costs of activity and can

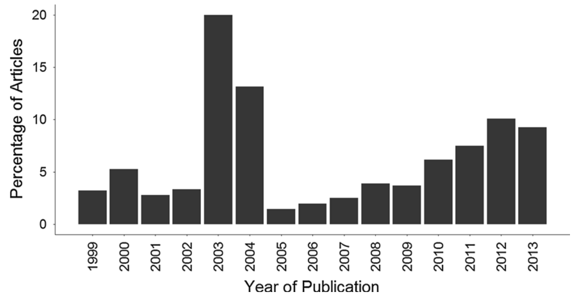


Fig. 1 Percentage of papers published in *Biological Invasions* incorporating physiology from the journal's inception in 1999 to the end of 2013. Percentages are derived from the number of articles that were identified in our literature search divided by the total number of articles published in each year

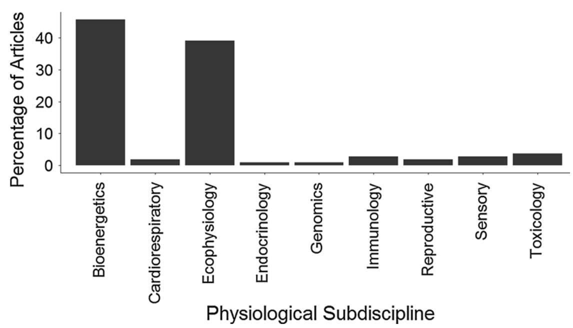


Fig. 2 Physiological subdisciplines used in invasion research published in *Biological Invasions*

therefore alter behavioural patterns or even gene expression (e.g. Roberge et al. 2008). Although changes to physiology may be more understated than extreme population declines or extirpations, they are useful for more rapid assessments of biological invasions.

When invasive species are introduced to a habitat where there is a niche already occupied, competition for resources such as territory and food supply may ensue (Mooney and Cleland 2001). The outcome of competitive conflicts can be explained using physiological metrics. For example, invasive turtles (*Trachemys scripta elegans*) have performance advantages over native competitors (*Mauremys leprosa*), reducing available thermoregulatory space (i.e. basking areas) for native turtles via exclusion competition (Polo-Cavia et al. 2012). Invaders can also have more direct effects on native species via predator–prey dynamics. Invasive alewife (*Alosa pseudoharengus*) in the Laurentian Great Lakes are believed to have contributed to the extirpation of native Atlantic salmon (*Salmo salar*) by creating a thiamine deficiency associated with high thiaminase in alewife, which became a prominent food source for salmon after introduction (Brown et al. 2005).

Physiological indices can be useful for evaluating interactions between invasive and native species. Using physiology to research the impacts of non-native species and describe their effects on local ecosystems can provide important information leading into management of invasions, particularly when predicting which species are likely to pose threats and become invasive and for tailoring management initiatives towards species that are likely to interfere with native community structure.

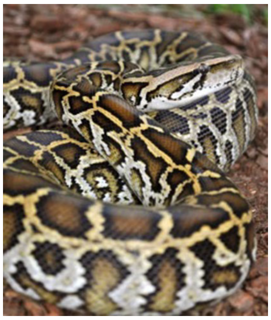
Predicting biological invasions using physiological tools

Management of invasive species is difficult, costly, and in many cases ambitious given the rapid spread of many successful invaders. Foreseeing invasion risk by characterizing attributes that relate to invasiveness is an important proactive approach to invasive species management (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001; Van Kleunen et al. 2010). The effective identification of potentially invasive species based on common traits is a central theme of invasion biology (Elton 1958; Williamson 1996; Kolar and Lodge 2001). For a variety of reasons, the majority of introduced species do not become invasive (i.e. the "tens rule"; Williamson and Fitter 1996). Ecophysiology, bioenergetics/nutrition, as well as endocrinology and gene expression can influence the ability to acclimatize to new environments and facilitate predictions about which species will become invasive.

Animal distribution is constrained by the environment, and environmental conditions such as temperature and salinity determine an animal's scope for metabolism, activity, and growth (Pörtner 2002). As a result, tolerance for local conditions can be used to estimate a species' likelihood of becoming invasive. Climatic tolerance is considered to be an important "ecological filter" (Olyarnik et al. 2009) and is a primary determinant of invasiveness for introduced species (Kelley 2014). Climatic tolerance is facilitated by physiological, cellular, and biochemical mechanisms and species with broad physiological tolerance are generally the most successful invaders (e.g. Marchetti et al. 2004; Kelley 2014) because they are more likely to be equipped for unpredictable

Box 1 Examples of successful integration between physiology and invasion biology for research and management objectives

The impacts of invasions on native species can be evaluated by measuring physiological status or performance of native species in the presence of invasive species. Graham et al. (2012) measured glucocorticoid stress hormone concentrations in fence lizards (*Sceloporus undulatus*) and found that individuals had high levels of circulating cortisol when they share territory with invasive fire ants (*Solenopsis invicta*). Identifying which species are most affected by the presence of an invasive species can be useful for informing management initiatives and focusing prevention efforts



Predicting biological invasions is difficult but is an important proactive approach to invasion management. Species distribution models (SDMs) can be used to forecast the spread of species across a landscape, which is useful for predicting which species are potentially invasive. Although many different variables can be used as predictors in SDMs, ecophyisological traits are important components (Rödder et al. 2009). For example, Rodda et al. (2009) used SDMs calibrated with physiological information on ecophysiology of Burmese pythons (*Python bivittatus*) across the mainland United States. To test whether the snakes could become invasive in South Carolina, Dorcas et al. (2011) conducted an experiment in an experimental enclosure to identify the thermoregulatory capacity of snakes experiencing thermal stress. Thus, both modeling and experimental techniques can incorporate physiology for predicting invasions

Preventative invasive species management aims to limit the introduction and spread of non-native species as a mechanism for reducing the likelihood that an invasive population will establish. Eurasian ruffe (*Gymnocephalus cernuus*) are native in Asia but were introduced to the Laurentian Great Lakes in the 1980s and rapidly spread throughout the lakes. The species is highly invasive and could establish in the Mississippi River drainage. To prevent Eurasian ruffe introduction in the Mississippi River would require reducing connectivity between the Great Lakes and the river, however, the Chicago Sanitary and Ship Canal is an important corridor for ships meaning that non-physical barriers were necessary to limit the movement of aquatic animals but not vessels. Dawson et al. (2006) tested the effectiveness of air bubble curtains and pulsed electric currents for deterring movement of Eurasian ruffe in captivity. The combination was postulated to be necessary for restricting movement of individuals across life stages. The barriers were ultimately ineffective, but demonstrate the utility of considering physiological mechanisms for preventing the introduction of invasive species.

Controlling invasive species that have established is often difficult, but various mechanisms exist for eradicating or maintaining invasive populations to limit impacts (Simberloff 2009) with both lethal and non-lethal methods. Double-stranded RNA engineering has interesting potential as a method for lethal control that is species specific. Ingestion of double-stranded RNA has been shown to be an effective method for killing insects (Whyard et al. 2009) as well as larval sea lamprey (*Petromyzon marinus*). Development of this tool could increase the effectiveness of control strategies for other invasive species and has the advantage of being highly species-specific

Photographs courtesy of Tracy Langkilde, Stephen Secor, and the Great Lakes Fishery Commission

environments. Environmental conditions are important components of species distribution models, which can be used to generate predictions about invasive species spread (Kearney and Porter 2009; Jiménez-Valverde et al. 2011). However, distribution modeling is optimized when considering ecophysiology rather than just environmental characteristics or natural history of a species (Rödder et al. 2009). Understanding where zones of physiological tolerance exist in a landscape can be used to focus management tactics: Tucker et al. (2012) suggested that shaded or turbid areas of Lake Tahoe could provide spawning refuge for non-native fish sensitive to UV radiation elsewhere in the lake. Accounting for physiological tolerance of species therefore not only increases the accuracy of distribution modeling but can be used at

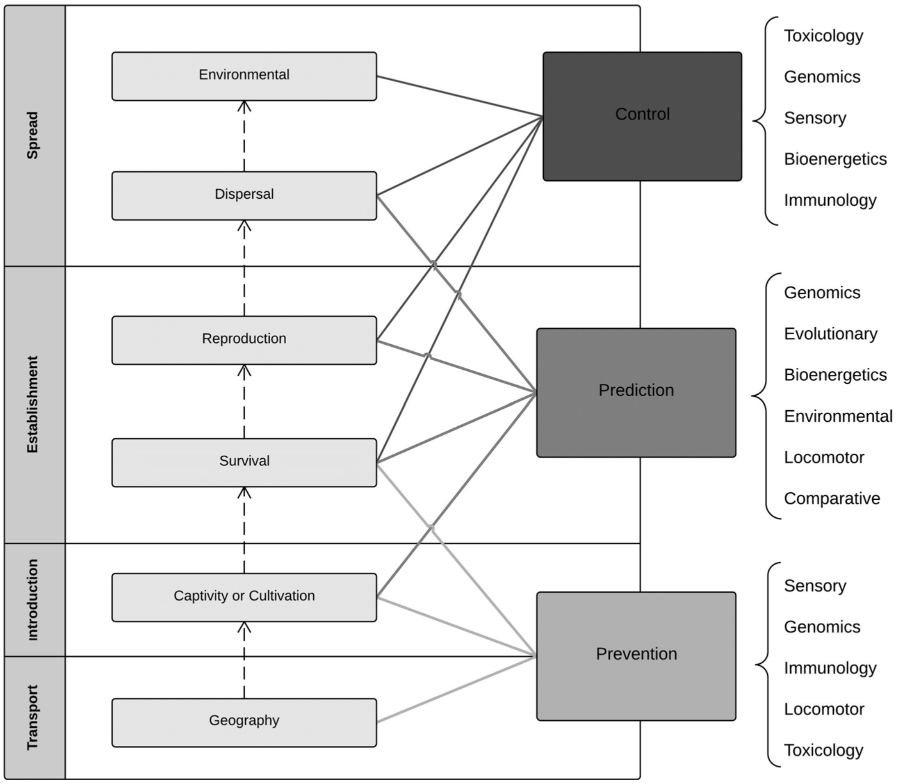


Fig. 3 Conceptual framework integrating physiological disciplines within invasive species management objectives: predicting invasions, preventing invasions, and controlling invasions (*shaded boxes*). *Hierarchical boxes* connected by *dashed arrows* represent barriers along the invasion process as introduced species establish as invasive. Intervention against invasions can be implemented with the help of physiological knowledge (see Table 1). *Shaded lines* show where intervention can be aimed with various physiological tools. Figure is adapted from components proposed in Blackburn et al. (2011). Methods with which each physiological discipline may be applied in order to mount a barrier are expanded on in Table 1. Graphics were compiled using lucidchart software

finer scales for informing prevention or control (see below; Fig. 3).

In addition to constraining activity and cardiac function, local climatic conditions influence the metabolic rate and nutritional requirements of introduced species. As a result, digestible and nutritious foods for animals to survive, mature, reproduce, and rear young are necessary for the establishment and spread of invasive species. Bioenergetic models that consider the biotic constraints of novel environments are important tools for predicting the spread of invasive species. Fish Bioenergetics 3.0 (Hanson et al. 1997), for example, can be used to model growth based on energetic requirements at different swimming speeds and water temperatures (e.g. Cooke and Hill 2010) and determine whether species will become invasive in a given range.

Stress associated with transport to a new environment can contribute to invasion success and the magnitude of stress experienced by animals introduced to new ranges can provide information about the likelihood that a species will establish. Many invasive species are introduced after transport or "hitchhiking" in a human vessel (e.g. in ship ballast water; Tamburri et al. 2002). Conditions during transport may be stressful, selecting for resilient species or individuals (Paiva 2014). Some invasive species have been shown to exhibit less extreme physiological responses in stressful situations whereas species that are not invasive exhibit higher stress in unfamiliar situations (Liebl and Martin 2012; Kelley 2014). Correspondingly, animals that have less sensitive immune responses (e.g. Lee and Klasing 2004; Lee et al. 2005), or heat shock proteins with lower induction temperatures (Kelley

2014), may have greater invasion success and dispersal capacity (Llewelyn et al. 2010) when introduced to novel environments. Stress hormones are useful for evaluating invasiveness in experimental conditions, for instance because stress can affect reproductive viability and reduce the likelihood of successful invasion (e.g. Moore et al. 2005). In general, animals that are successful invaders may be relatively proficient at coping with stress by regulating gene expression to compensate for adverse environmental conditions; transcriptional responses to heat or salinity stress are mechanisms that facilitate invasiveness of animals in otherwise hostile environments (e.g. Lockwood et al. 2010; Lockwood and Somero 2011). As a result, knowing how well a species adapts to stress can be useful for predicting whether it is likely to become invasive.

Predicting invasions is an important component of management and can benefit from identifying species that are liable to become invasive. Identifying physiological traits that might facilitate adaptation to local conditions or traits that might stereotype a species as a potentially invasive species can benefit from physiology. However, the utility of effective prediction depends on preventative mechanisms based on the information gathered from predictive methods or models.

Preventing biological invasions with physiological knowledge

Early identification or prediction of which species are likely to become invasive in a given range can inform preventative management of invasions. Even with good predictive models and knowledge of which species pose invasion risks, it is difficult to eliminate the introduction of all possible invaders across contexts given the large number of potential vectors. Instead, successful prevention aims to manage the number of individuals that are introduced and limit the viability of introduced populations that could become invasive. This means reducing introduction of individuals from potentially invasive species as well as limiting the viability of the invasive population prior to establishment during incipient invasions (von Holle and Simberloff 2005). Just as knowledge of a species' physiology can contribute to predicting its invasiveness, sensory physiology, genomics, toxicology, and locomotor physiology can be used to develop mechanisms or infrastructure for preventing invasions.

Physiology has already been used to generate best practices for management of invasion risks. For example, nitrogen injection into ship ballasts is a cost-effective technique for eliminating larval hitchhikers in ballast water (Tamburri et al. 2002). Introductions can also be limited by implementing barriers, which are an important preventative tool against invasive species and can be used to limit successful introduction, to decrease survival, or to inhibit reproduction in the novel environment by excluding individuals from accessing conspecifics or critical habitat. Physical barriers such as fences, cages, or water velocity are simple but can be effective for restricting movement. To some extent, physical barriers must consider the locomotor physiology and bioenergetics of target animals so that target animals cannot penetrate or circumvent the barrier (Day and MacGibbon 2007). However, physical barriers can be non-selective and are often not feasible, especially in aquatic environments where physical barriers would restrict ship passage (Noatch and Suski 2012). Non-physical barriers are an emerging alternative that exploit sensory physiology. Chemicals can be used to strategically influence movements and limit dispersal of animals, such as poisons that discourage movement across landscapes. However, poisonous chemicals can have unintended consequences for non-target species (Boogaard et al. 2003) or sensitivity may decrease over time (e.g. McKenzie et al. 2011). Alternative barriers that target sensory mechanisms have been developed for bycatch reduction in fisheries and could be applied to invasive species prevention, including aquatic strobe lights, bubble curtains, sonic and infrasonic recordings or blasts, mercury lights, or electric screens that are designed to influence the capacity or motivation to move (Goodson 1997; Taft 2000; Southwood et al. 2008; Stoner and Kaimmer 2008). The effectiveness of these preventive mechanisms often depends on species-specific strategies [e.g. specific sound frequencies (Noatch and Suski 2012), specific bubble spacing for bubble nets (Patrick et al. 1985)], as well as an understanding of the potential long-term effects on other species in the ecosystem. Some species may be attracted to the deterrent (Taft 2000), some individuals may be irreversibly damaged (e.g. blinded or deafened), whereas some individuals could acclimatize to the stressor, rendering it ineffective (Southwood et al. 2008).

Prevention is often an underutilized aspect of invasive species management (Simberloff 2009) and ineffective policy or deficient knowledge relating to invasiveness of introduced organisms can make it difficult to prevent invasions (Reaser et al. 2008). In some scenarios, preventative mechanisms are not enough to avoid the introduction or establishment of non-native species and incipient invasions move beyond the scope of prevention. When that happens, control measures such as eradication are necessary to manage the risk of an invasion (Lodge et al. 2006); these are addressed in the following section.

Controlling invasions with physiological concepts and tools

Given appropriate preventative measures and early detection, invasions can sometimes be prevented. However, in many scenarios, an invasive population becomes established and the invasion can only be controlled. Simberloff (2009) considers two important forms of invasion control: eradication and maintenance management. Eradication of established invasive species is difficult and may require considerable resources (Cacho et al. 2006). Alternatively, established populations of invasive species can be controlled to limit population density and mitigate impacts on ecosystems. Successful strategies aimed at controlling invasive species are complex, expensive, and multi-disciplinary. Often, the same techniques that are useful for eradication can be used to maintain an invasive population at low density (i.e. a technique used for population maintenance could also be used for eradication given sufficient effort). Moreover, techniques for invasive species control can benefit from incorporation of physiological concepts and tools such as developing tools for lethal control or reproductive inhibition as well as using physiology to inform and enhance efforts for trapping or biological control.

Lethal control using toxic chemicals is an effective means of managing invasive species. Chemicals may not be species-specific, such as rotenone, a common piscicide that prevents oxidative phosphorylation in gill breathing animals (Hollingworth 2001). As a result, non-target species are affected, resulting in collateral damage. Efforts can be made to develop chemicals that are more species specific and therefore minimize risk to non-target species (e.g. McDonald and Kolar 2007; Murphy et al. 2011). On land, this problem has been considered by wildlife managers when creating tainted baits for invasive species (e.g. Jessop et al. 2013). Using chemicals that target a specific physiological mechanism and using baits that are attractive to specific species can increase the effectiveness of these control strategies (e.g. Pitt and Witmer 2007; Lapidge et al. 2007).

An alternative strategy to lethal control can be disrupting successful reproduction using chemicals. Rapid reproduction and high fecundity are life history traits that can make some invasive species difficult to control (Ricciardi and Rasmussen 1998), rendering reproductive suppression a useful method for reducing population viability of invasive species. Although it is often difficult to gain public approval for tools that interfere with reproduction (Thresher and Kuris 2004), they represent a good alternative to lethal control, which may itself be controversial (Barfield et al. 2006; Kirkpatrick et al. 2011). Contraceptives have been developed for over 85 wild animal species, and although species-specific strategies can be necessary, comparative physiology can potentially allow lateral application of some solutions to species with similar physiology (Kirkpatrick et al. 2011). Immunocontraception is a promising avenue for controlling the spread of invasive species, and several useful strategies have been developed, such as genetically modified viruses that kill or sterilize infected individuals and autocidal technologies that bias sex ratios toward males (Thresher 2008). For established invasive species, contraceptives can be used (Mayer et al. 2002). However, there are challenges such as how to effectively deliver contraceptives to target species (Humphrys and Lapidge 2008).

When effective delivery of chemicals is difficult, such as when target species are widespread or use heterogeneous habitat with refuge from poison, attracting animals into traps or toward poisoned baits can be effective and semiochemicals can lure animals into traps (Wagner et al. 2006; Morris and Whitfield 2009; Yavno and Corkum 2010; Crossland et al. 2012). Other sensory cues have been identified and mimicked for managing invasions, such as electrophysiochemical signals for persuading emerald ash borer (*Agrilus planipennis*) pests into traps (Crook et al. 2008). Visual stimuli can also be useful for attracting or repelling insects (Rieske and Raffa 2003; Demirel and Yildirim 2008). Sensory manipulation can provide effective enhancements to control strategies, but genomic tools may eventually provide more effective methods for invasive species management. Oral delivery of double-stranded RNA, which targets vATPase transcript genes, has been determined to be an effective lethal alternative to poisons for a variety of crop pests as well as sea lamprey (Whyard et al. 2009; Heath et al. 2014). The advantage of this RNA interference technique is that it is highly species specific.

The introduction of non-native predators, competitors, parasites, or pathogens, known as biological control (Santha et al. 1991), can be a useful method for managing invasive species. However, biological control can be controversial (Simberloff 2012) given the potential to create new problem species (Messing and Wright 2006). The presence of biological control agents is intended to adversely affect the fitness of invasive species by impairing performance, which can be measured using a variety of physiological metrics (e.g. Marr et al. 2010). To avoid potential impacts on non-target species, bioenergetic and immunological assessments can provide information about the potential side effects of biological control. For instance, biological control with lungworm and lipopolysaccharide bacteria is being considered for cane toads in Australia given that the effects of the parasites are not lethal for native tree frogs (*Litoria caerulea*) relative to cane toads (Pizzatto and Shine 2011; Pizzatto and Shine 2012).

Managing invasive species using lethal or non-lethal control is difficult and costly. However, many techniques used for controlling invasive species can benefit from the incorporation of physiology because physiological data about the sensitivities of invasive animals can be manipulated for improving control strategies. Proactive measures can be used to help tailor management initiatives to species that are likely to have negative impacts; moreover, increased reliance on prediction and prevention can reduce the need for control (Simberloff 2009; see above; Box 1).

Synthesis

Utilization of physiological knowledge for informing invasive animal management is not a new concept (Box 2), but there are opportunities for further integration. Physiology is fundamental to invasion biology because it regulates an animal's response to its environment (Pörtner 2002) and is characterized by a variety of related domains that focus on mechanistic responses of organisms (Wikelski and Cooke 2006; Cooke et al. 2013), many of which are already established contributors to invasion science (Table 1). Physiology is just one lens through which to view biological invasions, and is most useful in concert with other approaches including population dynamics, ecology, and behaviour. However, the advantage of applying physiological tools is that it provides a mechanistic explanation for higher organization-level processes to individual animals. As a result, physiological metrics can provide rapid information about the effects of invasions. Further application of physiological knowledge and the development of physiological tools should afford invasive species managers with the opportunity to manage risks associated with certain species that may invade and develop preventative and control measures for managing invasions.

The literature review of *Biological Invasions* provided insight into the extent to which physiology is presently used within invasive species research, albeit with a cursory view of invasion literature. Integration of physiology within invasive species research and management has been considered in many forms but is not necessarily consistently increasing, given that 2003 and 2004 had the highest frequency of papers that incorporated physiology. As a result, there is potential for increased adoption of diverse physiological tools within invasive species research (see Table 1). Indeed, we found that the vast majority of studies considered ecophysiology or energetics and only few studies considered other physiological tools. Studies that addressed ecophysiology often measured tolerance ranges of invasive species, particularly to explain why a species had successfully invaded. Most studies that incorporated physiology did so in articles that explained or described invasion events and few articles addressed management objectives explicitly. Explaining invasions can be applied to predicting future invasions (i.e. identifying which species tend to be invasive or which traits characterize invasive species); however, not all studies made the link to this potentially relevant management objective. Furthermore, many other relevant applications for physiology were infrequently

Box 2 Asian carp are a relevant example of the utility of physiological tools in invasion science. The potential economic consequences of their invasion have inspired a variety of creative solutions to prevent their spread within North America. Here we present an integrated example of using physiology for studying and managing invasive Asian carps in the Mississippi River drainage and Laurentian Great Lakes. Photograph courtesy of Stephanie Liss

Asian carps (e.g. *Hypophthalmichthys nobilis*, *molitrix*) are invasive fishes spreading northward through the Mississippi River drainage. Comparison of body condition indicates that the presence of the invasive species is negatively affecting the nutrition of native gizzard shad (*Dorosoma cepedianum*) and bighead buffalo (*Ictiobus cyprinellus*) in the Illinois River (Irons et al. 2007). Efforts made to stop the spread into the Laurentian Great Lakes have benefited from incorporation of physiology. Bioenergetic models have been used to assess the risk of invasion on phytoplankton density (Cooke and Hill 2010). Development of preventative measures for stopping the spread of carp from the Mississippi drainage into the Laurentian Great Lakes have incorporated physiological knowledge, including a large non-physical electric barrier that eliminates fish passage (Sparks et al. 2010) as well as bubble curtains to dissuade dispersal (Zielinski et al. 2014). Research is also underway to develop methods to manage populations of Asian carp and inhibit establishment and spread by developing species-specific piscicides (e.g. that exploit high levels of trypsin in guts of Asian carp that can be used to release poisons and ensure targeted delivery; Anon 2014) and pheromonal attractants (Stokstad 2010), which can be used to lure individuals into traps. Sequencing of the genome may yield further information for controlling incipient Asian carp invasions via the development of DNA interference technology (e.g. Heath et al. 2014)

addressed by the studies we identified (see Table 1 for highlighted examples of how diverse physiological tools can be implemented).

Consistent with the definition of conservation physiology (see Cooke et al. 2013), any study that considered physiology was included in our quantitative review, even those that did not focus on physiology or necessarily use physiological tools for studying invasions. New tools that are available for conducting physiological assessments for conservation studies may facilitate increased integration between invasion science and physiology moving forward (Costa and Sinervo 2004). The use of portable point-of-care equipment for analyzing blood samples in the field is an emerging technology that allows rapid insight into stress status of animals (Stoot et al. 2014). Blood based physiological parameters change in response to stress and can therefore provide information about the response of a non-native species to a new environment or a measurement that identifies sublethal effects of an invasive species on native species. Stoot et al. (2014) reviewed examples where these devices have been used for fish, mammals, birds, and turtles, and they show that they have the potential to provide rapid information to scientists studying invasions, which is important given that time is often a limiting factor when seeking to manage invasions effectively. Point-of-care devices can offer good physiological insight, but require capture of animals for blood sampling, which can be time consuming and may exacerbate stress. Alternatively, methods are developing for remotely sampling stress hormones in the field (e.g. in cane toad urine; Narayan et al. 2011). In addition, physiological tools are increasingly being integrated with biotelemetry tags for studying free-living animals, which can be used to offer unprecedented insight and provide physiological data about animals in the wild. For example, Dorcas et al. (2011) used thermal loggers to evaluate how non-native Burmese pythons (*Python bivittatus*) adapted to lethal temperatures in South Carolina and predict whether they posed an invasion risk. Integrating electronic tagging tools for measuring physiology will likely enable further advances in the field of invasion science.

Under changing climatic conditions, invasive species could pose an increasingly prominent conservation threat (Dukes and Mooney 1999). Many aquatic species already operate near their upper thermal limit at which physiological performance declines (Iftikar et al. 2014), and temperature increases are likely to result in performance decreases for many native species. In areas where the environment is relatively stable, animals are adapted to local temperature regimes, reducing maintenance costs (i.e. the ability to tolerate a wide range of temperatures is energetically expensive; Pörtner and Farrell 2008). Changing climatic conditions can drive range shifts (Walther et al. 2002) and provide an advantage to non-native species that have broader tolerance to changing conditions (e.g. in aquatic systems; Sorte et al. 2013). Huang et al. (2011) found a significant relationship between settlement of invasive species and increasing temperature; with projected increases in temperature resulting from climate change, ecophysiology will provide an important parameter for predicting invasions using distribution modelling. Furthermore, given that the impacts of invasive species are often evaluated at the ecosystem or landscape level, there remains a great potential for the integration of physiological tools within the realm of landscape ecology and macrophysiology (Chown and Gaston 2008; Ellis et al. 2011).

Given that biological invasions are liable to become an increasing threat to conservation efforts, prevention is poised to represent a more important priority. Simberloff (2009) points out that controlling established invasive species can be ineffective and expensive relative to preventative measures but that management agencies are more reluctant to engage in prevention than in control. Naturally, preventing invasions is difficult and requires understanding about the likelihood that species will become invasive so that preventative efforts can focus on relevant species. Although physiology provides considerable relevant information about the sensitivities of animals that can be used for prevention (Box 1), we were able to identify relatively few examples where preventative measures have benefited from physiological knowledge.

Biological invasions represent a challenge to biodiversity conservation and an integrated approach is necessary for researching and managing invasive species. There is likely to be a growing synergy between invasive species management and diverse subdisciplines within physiology (see Table 1) because physiology provides some relatively unique and efficient tools for invasion scientists. Much of the physiological data and knowledge necessary for managing invasions is already available and opportunities are expanding with technological advances (see Box 2). Physiology is ideally positioned to contribute to invasion science given that management is most effective prior to the establishment of invasive species and that physiology lends well to rapid assessment. Moving forward, there is great potential for physiological tools to become standard for assessing, predicting, preventing, and managing invasive species. Indeed, invasive species research and management will hopefully benefit from an enhanced synergy with physiology in the coming decades.

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