The Future of Invasion Science Needs Physiology

LEIGH BOARDMAN, JULIE L. LOCKWOOD, MICHAEL J. ANGILLETTA JR, JESSE S. KRAUSE, JENNIFER A. LAU, MICHAEL E. LOIK, DANIEL SIMBERLOFF, CHRISTOPHER J. THAWLEY, AND LAURA A. MEYERSON

Incorporating physiology into models of population dynamics will improve our understanding of how and why invasions succeed and cause ecological impacts, whereas others fail or remain innocuous. Targeting both organismal physiologists and invasion scientists, we detail how physiological processes affect every invasion stage, for both plants and animals, and how physiological data can be better used for studying the spatial dynamics and ecological effects of invasive species. We suggest six steps to quantify the physiological functions related to demography of nonnative species: justifying physiological traits of interest, determining ecologically appropriate time frames, identifying relevant abiotic variables, designing experimental treatments that capture covariation between abiotic variables, measuring physiological responses to these abiotic variables, and fitting statistical models to the data. We also provide brief guidance on approaches to modeling invasions. Finally, we emphasize the benefits of integrating research between communities of physiologists and invasion scientists.

Keywords: invasion biology, prediction, mechanism, modeling, demography

Both purposeful and accidental introductions of nonnative species have a long history, occurring before 1500 and accelerating thereafter (di Castri 1989, Seebens et al. 2018). Many of these nonnative species produce negative effects that ripple through social, cultural, and ecological systems (Ricciardi et al. 2013, Blackburn et al. 2019). These events have spurred substantial interest in how nonnative species cause their impacts and in tools for predicting, preventing, or lessening these impacts (Lodge et al. 2016). Despite research efforts and policies aimed to limit invasions, introductions of nonnative species have accelerated globally (Seebens et al. 2018). Thousands of nonnative species are introduced annually around the world, qualifying species invasions as one of the major agents of global environmental change in the coming decades (Pyšek et al. 2020, Ricciardi et al. 2021). This acceleration is clustered in nations that have expanded international commerce and trade routes or experienced rapid climate change (Seebens et al. 2018, Ricciardi et al. 2021). Often, these regions were minimally affected by nonnative species in the past (e.g., tropics, poles; Mead et al. 2011, McCarthy et al. 2019). Furthermore, the species now invading these regions belong to different taxonomic groups than more typical invasive species (e.g., a shift from birds and fishes to insects and cnidarians; Wilson et al. 2009, Bellard et al. 2013; and see Essl et al. 2015). Importantly, the geographical regions likely to experience greater future introductions belong to countries less economically able to address this problem (Early et al. 2016, Sardain et al. 2019).

The application of physiological principles to diverse fields has revealed novel answers to vexing questions about the evolution and persistence of biodiversity, especially in the face of global changes (Ricklefs and Wikelski 2002, Holway and Suarez 2006, Deutsch et al. 2008, Kearney et al. 2008, 2009, Sinervo et al. 2010, Skultety and Matthews 2017). In this article, we consider physiology to be processes at the individual level that arise through an organism's interaction with its environment, including basic processes such as resource acquisition, thermoregulation, responses to stress, and phenology. The insights that physiology provides to invasion science rest on acknowledging the constraints on fitness imposed by environmental conditions that determine whether an introduced nonnative population becomes invasive (Lennox et al. 2015). Motivated by the search for the rules of life underlying biological invasions (Meyerson et al. 2019), we provide a framework for incorporating physiology into research to predict the transport, introduction, establishment, and spread of invasive species. In particular, we address how the trove of existing data from physiological experiments can be applied to forecasting fitness outcomes for nonnative organisms, and we identify the types of physiological data that invasion scientists need most. The needs of invasion science require careful consideration and, in some cases, modifications to traditional physiology experimental designs to better understand how physiological processes

BioScience XX: 1–16. © The Author(s) 2022. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com
https://doi.org/10.1093/biosci/biac080

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

enable species to establish and become invasive. Reciprocally, biological invasions provide natural experiments that may benefit physiologists by enabling the study of phenotypic plasticity as nonnative species move to novel environments and by comparing physiological traits between organisms in their native and invaded ranges (e.g., Parker et al. 2003, Wingfield et al. 2015; for discussions, see Sexton et al. 2009, Engel et al. 2011, Atwater et al. 2018, and Hodgins et al. 2018).

The major goals of invasion science are to predict which species are likely to establish self-sustaining populations outside their native range, to determine which of these established species will spread to surrounding regions, and to assess how these species will affect native ecosystems or human societies. To meet these goals, at the United States National Science Foundation (NSF)–funded Rules of Life Underlying Biological Invasions workshop (Meyerson et al. 2019), we agreed that we must account for the following: the relationships among environmental stress, physiological responses, and fitness (with stress defined in the present article as extreme physical conditions that lead to injury, illness, malnutrition, or dehydration); behavioral responses to environmental cues; evolutionary responses to novel environments; changes in species' fundamental niches in novel environments; fitness outcomes of ecological interactions; and the impacts of ongoing environmental change, including climate, on all of the above.

Physiologists address aspects related to each of these topics, although usually outside the context of invasions. In particular, findings from cell or systems physiology, ecological physiology, evolutionary physiology, and conservation physiology can be pertinent for invasion science (Chown and Gaston 2008, Lennox et al. 2015). Several of the clusters of hypotheses and frameworks within invasion biology recently defined by Enders and colleagues (2020) can be viewed through the lens of physiology (table 1). The most relevant of these clusters is the trait cluster, which contains hypotheses that focus on traits that explain which nonnative species become invasive (i.e., traits associated with invasiveness; box 1; Pyšek and Richardson 2007, Van Kleunen et al. 2010, Capellini et al. 2015, Mahoney et al. 2015). However, knowledge of physiology can inform invasion science across all stages of an invasion—from transport and introduction to establishment and spread (figure 1; Blackburn et al. 2011).

Below, we argue that integrating physiology and invasion science can produce a necessary and substantial step toward broadly applicable and powerful approaches to reducing invasion risk and minimizing invasion impacts. By targeting physiologists who do not currently work on invasions and invasion scientists who may not recognize the value of physiological data, we aim to broaden the inclusion and usage of plant and animal physiology data in invasion science. We start by providing an overview of the different stages of the invasion process and give examples of how the partition into stages is relevant. For a retrospective look at how physiology has been integrated with invasion, in the framework of prediction, prevention, and control, see Lennox and colleagues (2015). To move invasion physiology forward, we then provide a framework for experimental design to ask questions about physiology through a demographic lens and discuss modeling demographic data and the current limitations of this approach.

Invasion science through a physiological lens

Transport. The transport of individuals from their native to nonnative habitats initiates invasion. If these individuals survive transport, they may be introduced (Blackburn et al. 2011). Understanding patterns in transport of nonnative species is increasingly seen as key to forecasting invasions accurately as global trade shifts in response to climate change, market forces, political alliances, and technological innovations (Sinclair et al. 2020). During transport, an organism is entrained in a transportation vector (e.g., ship, cargo hold, crate), where it may experience a wide range of conditions, including those that clearly impose substantial physiological stress (Briski et al. 2014, Sinclair et al. 2020). For example, individuals of nonnative species moved in the water of a ship's ballast experience darkness, toxic chemicals, changes in salinity, and extreme heat or cold for days or even weeks (Wonham et al. 2001, Piscart et al. 2011). However, invasion science is just beginning to articulate and test models of invasion probability in the transport stage (Sinclair et al. 2020), providing an opportunity for physiologists to contribute to this effort.

Understanding how organisms cope physiologically during transport can highlight the broader importance of physiological processes for survival. For example, knowing how organisms resist thermal extremes or balance pH during transport would help to predict whether nonnative organisms can survive the transport stage (figure 1; e.g., Karsiotis et al. 2012, Lenz et al. 2018). Such knowledge also informs efforts to reduce invasion rates by targeted treatments and biosecurity protocols. For example, knowledge of physiology has played a key role in risk assessments (e.g., hypoxia tolerance and visual systems in Indo-Pacific lionfish *Pterois* spp., Hasenei et al. 2020; thermal tolerance and cellular stress markers in Indo-Pacific damselfish *Neopomacentrus cyanomos*, Tremblay et al. 2020) and devising prevention and control strategies, including exchange of water between ballast and ocean (Hallegraeff et al. 1997), heat treatment of wood crates to kill emerald ash borer (Sobek et al. 2011), and modified atmosphere treatments of fresh commodities to remove insects (Chen et al. 2020).

Introduction to novel habitats. Individuals that survive transport may face carryover effects from the stress of transport, compounded by challenges of a novel environment. For example, many species are released in a weakened state following transport, making them susceptible to death from illness or starvation (Briski et al. 2014). Resources and conditions on release can range from being advantageous to benign and

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Table 1. Clusters of hypotheses and frameworks in invasion biology (as defined by Enders et al. 2020) and how they relate to physiology.

Cluster	Basic description with list of hypotheses	Physiological research examples
Biotic interaction cluster	These hypotheses involve the role of interspecific interactions in determining invasion success. Many of these hypotheses assume that when a species is introduced to a new environment, it lacks natural enemies, which allows it to gain an advantage and thrive. – Biotic indirect effect[a] – Enemy inversion – Enemy of my enemy aka accumulation of local pathogens hypothesis – Enemy reduction – Enemy release – Evolution of increased competitive ability – Increased resource availability[a] – Missed mutualisms – New associations – Reckless invader aka boom–bust[a] – Resource–enemy release[a] – Shifting defense hypothesis – Specialist–generalist	Nutritional stoichiometry Physiological weapons or defenses (e.g., production of toxins) Digestive physiology (e.g., regulation of machinery for digestion and transport) Muscle physiology for a predator's ability to capture prey and the prey's ability to evade predators Immunophysiology for host–pathogen interactions Developmental physiology for mutualists (e.g., uptake of and acclimation in response to coral symbionts) Plant defense traits (phytochemistry, carbon to nitrogen ratio, trichomes)
Darwin's cluster	Hypotheses relating to evolutionary views on invasion biology. These highlight that an organism's evolutionary history can determine the outcome of biotic interactions. – Biotic acceptance – Biotic resistance – Darwin's naturalization – Ecological imbalance – Ecological or evolutionary naivety – Empty niche[a] – Island susceptibility hypothesis – Limiting similarity	Specialists versus generalists with respect to abiotic tolerances (width of fundamental niche) depends on evolutionary history in native range; generalists seem more likely to become invasive The breadth of physiological tolerance also relates to the potential for adaptation to novel environments (Huey and Kingsolver 1993)
Propagule cluster	The focus of these hypotheses is that the number of introduced nonnative species is related to the probability of becoming invasive. – Colonization pressure – Global competition – Human commensalism[a] – Invasion meltdown – Propagule pressure – Sampling – Tens rule	Biomechanics and associated physiology on plasticity related to dispersal morphs or phases
Resource availability cluster	Invasion success is determined by access to resources, which is affected by abiotic and biotic conditions and their interactions (Catford et al. 2009). – Disturbance – Dynamic equilibrium model – Empty niche[a] – Environmental heterogeneity – Human commensalism[a] – Increased resource availability[a] – Opportunity windows – Reckless invader aka boom–bust[a]	Physiology of resource specialists versus resource generalists. Energetics, e.g., allostasis model (Wingfield et al. 2015) Plant growth and allocation
Trait cluster (nested in Darwin's cluster)	Hypotheses that focus on certain species traits that explain why a nonnative species becomes invasive (i.e., traits that are associated with invasiveness; Pyšek and Richardson 2007, Van Kleunen et al. 2010, Capellini et al. 2015, Mahoney et al. 2015). – Adaptation[a] – Habitat filtering[a] – Ideal weed[a] – Novel weapons[a] – Plasticity hypothesis[a] – Polyploidy hypothesis[a]	Abiotic stress tolerance, physiological plasticity (acclimation studies), energetics, locomotion. See box 1.

Note: For a list of physiological disciplines that contribute to the study or management of biological invasions, see Lennox and colleagues (2015). [a]The hypothesis relates to multiple clusters.

could even guarantee immediate death (Briski et al. 2014). Individuals may enter abiotic conditions that lie at the extreme ends of their physiological tolerances. For example, aquarium trade fish species are frequently released by their owners into the environment (Lockwood et al. 2019). Often, these species are native to tropical or subtropical freshwater or marine ecosystems, but they are sold, kept, and eventually released into other ecosystems (Duggan et al. 2006). Their

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Box 1. One trait value to rule them all?

Invasion hypotheses that incorporate physiology primarily focus on traits associated with invasiveness (a trait cluster; Enders et al. 2020). Many risk assessments or invasion hypotheses assume that certain traits predict invasion success. However, a common misconception is that individuals or populations of invasive species are genetically uniform or respond to all environmental conditions similarly (Cronin et al. 2015). In reality, specific traits likely aid success across each invasion stage and in different environments. For example, traits that enhance tolerance of extreme abiotic conditions would promote success during transit, but the potential to develop and reproduce rapidly would promote establishment. Similarly, although a trait such as early flowering would be advantageous at high latitudes, delayed phenologies and increased allocation to vegetative growth many be advantageous at low latitudes (Colautti and Barrett 2013). Finally, traits are not static (e.g., Luong et al. 2021). The environment can influence trait expression, and natural selection or genetic drift can alter the mean phenotype during invasion, potentially supporting or hindering further spread (for a review, see Whitney and Gabler 2008). Studying invasive species only in the invaded range risks missing important information about tolerance of abiotic conditions (i.e., freezing) that could be gleaned by studying it in its native range (Griffith et al. 2014).

We should also recognize that traits vary across the native range, so the success of an invasive species in its nonnative range could depend on abiotic conditions in the specific place of origin of founding individuals. Even within a species, genomic traits influence physiological traits and fitness outcomes. For example, a wide diversity of conditions favor one genotype of *Phragmites australis* over another (Eller et al. 2017, Meyerson et al. 2020), and intraspecific variation in *P. australis* genome size and ploidy level influences plant traits and fitness within its invasive range (Meyerson et al. 2016a, Pyšek et al. 2018, 2020). Integrating knowledge of plant traits such as genotype or genome size with physiology and with forecasts of global climate change can help predict how plant populations will respond to selective pressures by range changes (Suda et al. 2015).

The invasion of European green crabs (*Carcinus maenas*), first recorded in 1817 in the United States, provides a classic example. Green crab populations gradually expanded northward to the Bay of Fundy after their initial introduction, stalled there, but spread suddenly into the much colder Canadian Maritimes in the 1980s. This range expansion, originally attributed either to warming sea temperatures or to adaptation to cold water, was later connected to the introduction of a second population of founders in the Canadian Maritimes, likely originating from the northern end of the crab's native range in Europe (Roman 2006). Therefore, this range expansion was due not to selection within the newly established nonnative range but, rather, to selection in the native range for a cold-tolerant ecotype released in Canada (for a review, see Tepolt 2015). This possibility could have been inferred from a model that incorporates physiology, because studying the thermal tolerance of the nonnative species at low latitudes would lead one to conclude that northern expansion to the Canadian Maritimes would be impossible for the genotypes initially introduced.

Likewise, an invasive species that has spread widely after an initial introduction may perform differently across latitudes in its nonnative range because environmental conditions differ. For example, in eastern North America, the macrophyte *P. australis* has established from Quebec and Ontario to southern Florida and Louisiana. Native plant communities are more susceptible to invasion by *P. australis* at lower latitudes, because of different latitudinal gradients in herbivory for native and nonnative genotypes (Cronin et al. 2015).

survival after release depends on whether these individuals tolerate extreme levels of temperature, oxygen, and salinity stress. For example, the potential for dispersal of the round goby (*Neogobius melanostomus*) into novel environments is dictated by the relationship of high salinity to the fish's aerobic metabolism and osmoregulatory capacity (Behrens et al. 2017). However, in some instances, tolerance limits based on the species's native range are not limiting factors, such as when Pacific lionfish survive low salinity water conditions in Florida (Jud et al. 2015). Therefore, physiological processes relevant to the introduction stage include development or acclimation needed to survive in the novel environment (e.g., phenotypic plasticity, figure 1; see Lennox et al. 2015).

Establishment. After introduction, nonnative organisms must establish a self-sustaining population that may grow and disperse. In all cases, the survival, growth, and reproduction of individuals just after introduction determine whether a nonnative species will establish a population. Because germination (for plants), survival, and fecundity are key demographic traits for establishment, physiological research relating to germination, nutrition, and endocrinology are particularly relevant (figure 1; see Lennox et al. 2015).

The study of establishment has seen the most integration between invasion science and ecological physiology, particularly through building correlative and mechanistic niche models for invasive species (Thuiller et al. 2005, Pyron et al. 2008, Griffith et al. 2014) and testing for contemporary evolution in the face of rapid environmental change (Sotka et al. 2018). For example, a species distribution model that described the dependences of physiological rates (growth, respiration, carbon and nitrogen uptake) on environmental factors (soil nitrogen, soil water, solar radiation, and temperature) was used to assess invasion risk for Australian acacia and eucalypt tree species (Higgins and Richardson 2014). Similarly, release from ecological enemies such as predators, pathogens, and parasites is commonly invoked to explain why nonnative species quickly establish a population and eventually become common (Blossey and Notzold 1995, Keane and Crawley 2002). Enemy release may result in evolutionary increases in competitive ability or other traits that promote invasion as natural selection may favor

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

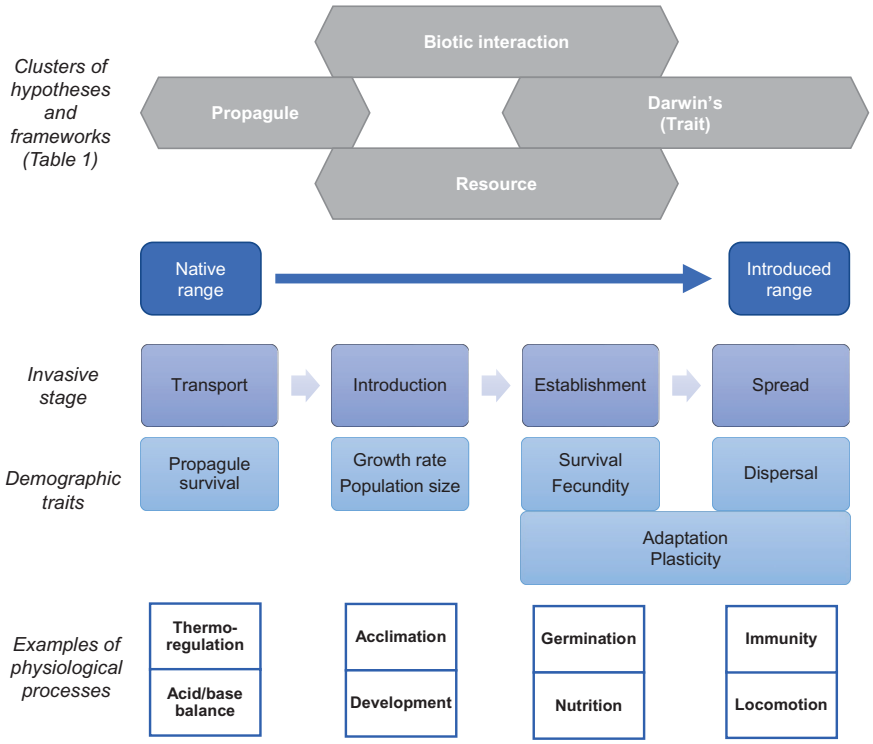

Figure 1. Links among invasion hypotheses and frameworks (Enders et al. 2020), invasion stages (Blackburn et al. 2011), demographic traits, and underlying physiological processes. The transport stage from native to nonnative habitats initiates the invasion. Individuals that survive transport face challenges of survival in a novel environment. The next step in the invasion requires nonnative individuals to establish a self-sustaining population, before the new population may finally spread, negatively affecting native ecosystems and their ecosystem services (Blackburn et al. 2011). Different demographic traits are associated with each invasion stage, with several physiological processes underlying these traits. The physiological processes are interlinked, and many will affect various demographic traits along the invasion pathway, based on the specific organisms and their abiotic and biotic interactions. See Lennox and colleagues (2015) for a detailed list and examples of physiological processes that have been used to inform invasion.

individuals that divert energy and resources away from costly defenses and toward growth (e.g., Rotter and Holeski 2018). Nevertheless, substantial gaps exist in integrating invasion science and ecological physiology, stemming from a fundamental difference in how and why physiological data are gathered (see below).

Spread. Some nonnative species that establish self-sustaining populations may spread broadly beyond their initial location of establishment, earning the moniker *invasive* (Blackburn et al. 2011). Even if the site of release presented few physiological hurdles, the spread of the population across the landscape will force individuals to confront novel abiotic conditions and biotic interactions. Among other processes, during this invasion stage, immune responses, energetics, and locomotion may determine an invasive species's spread and subsequent impact (figure 1; see Lennox et al. 2015). Comparing the physiology of the nonnative species with that of their native congeners can help to predict environmental conditions that promote persistence or spread of nonnative species (e.g., Lockwood and Somero 2011, Cortes et al. 2016). In some cases, spread may require or benefit from adaptation to novel environmental conditions (e.g., photoperiods, Colautti and Barrett 2013; temperature, e.g., Card et al. 2018; or latitudinal clines, e.g., Huey et al. 2000) or may be facilitated by the evolution of traits that promote dispersal (Shine et al. 2011; e.g., Ochocki and Miller 2017).

Management and impacts. Finally, mechanistic links among physiology, fitness, and ecological impacts can inform management of invasive species (Lennox et al. 2015), similar to the benefits of using physiology to improve predictions of how organisms will fare in novel environments for conservation biology (Cooke et al. 2013, 2020). For example, knowledge of physiology has played a key role in devising strategies to control or eradicate invasive species, including the sea lamprey *Petromyzon marinus* (Siefkes 2017).

As nonnative species increase in abundance and spread across the landscape, the fitness of native species they encounter is likely to be affected. Invasive species can affect the physiology of native species through various ecological interactions, including releasing toxins, consuming resources, and inducing the defenses and hormones associated with parasitism, herbivory, or predation (Ricciardi et al. 2013). The degree to which individuals of native species suffer a fitness consequence of their interactions with nonnative species provides a mechanistic explanation for why affected native populations decline and, ultimately, why some native species are lost and how ecosystems are altered (Cameron et al. 2016).

Building an integrative invasion-physiology science

The primary outcome of greater integration of physiology with invasion science is the ability to predict invasions in

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

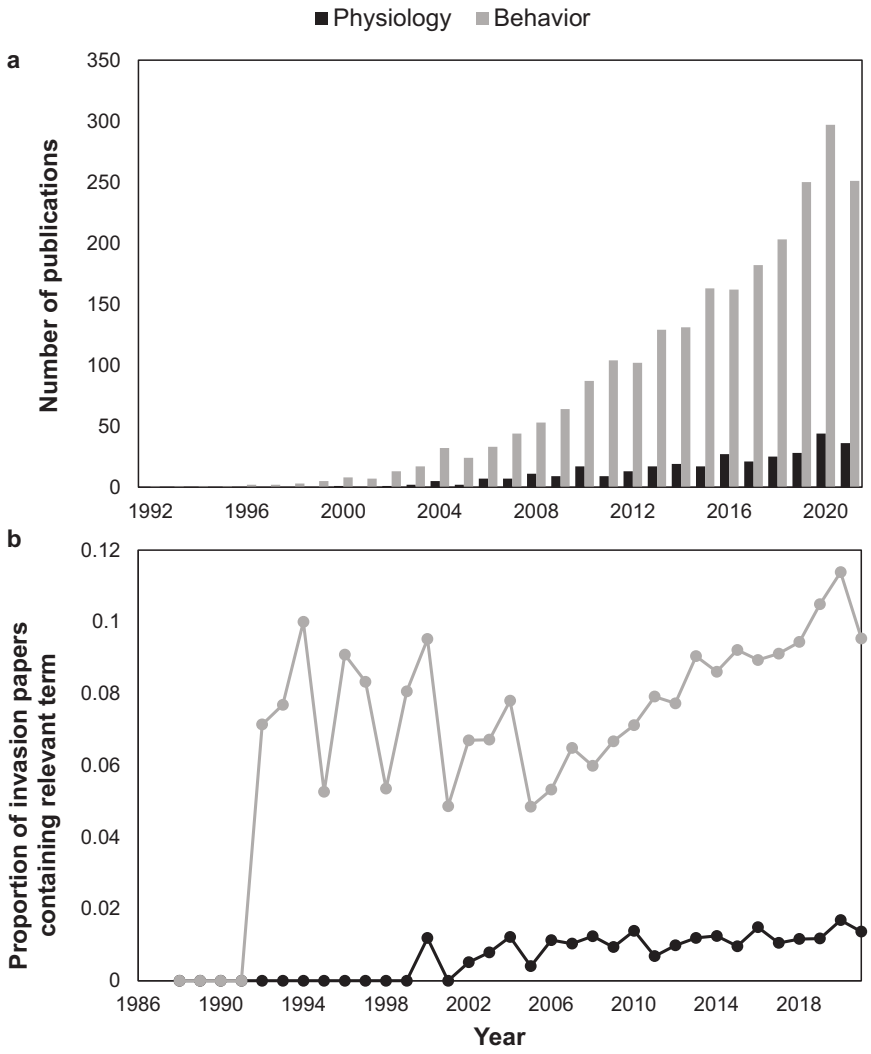

Figure 2. (a) Studies applying physiological perspectives to the study of invasive species are increasing. Histogram shows breakdown of the results of a Web of Science Core Collection topic search on 8 February 2022, including the terms* "invasion biology" or "invasive species" or "biological invasion" and "physiology" *(the black bars, total* n *= 318). For comparison, we repeated the search replacing* "physiology" *with* "behavior" or "behaviour" *(the grey bars, total* n *= 2371). (b) We also scaled the data for both physiology and behavior papers as a proportion of the total number of invasion papers (*n *= 27,100) for each publication year.

diverse contexts. Data from "model" organisms often inadequately describe the invasion process, possibly because true model species are limited (Crystal-Ornelas and Lockwood 2020). This process is also poorly predicted by empirical evidence or theoretical models produced for only one invasion stage (Uden et al. 2015). Certainly, as we look toward a future in which invasive species continue to arise from global trade, and although the global environment continues to change, we cannot assume the hypotheses and insights from yesterday provide adequate forecasts of the future (Ricciardi et al. 2021). In the coming sections, we provide more detailed guidance for integrating physiology with invasion science and what this integration could mean for the future of each discipline.

Applying physiology to research on biological invasions is increasingly common but still relatively rare, with ecological physiology and bioenergetics being the most common physiological subdisciplines in invasion research (Lennox et al. 2015). On the basis of a search of the Web of Science, using the terms *"invasion biology" or "invasive species" or "biological invasion" and "physiology,"* the first studies combining physiology with the study of invasive species appeared in 2000, and only 318 papers have been published on this topic since (up to and including 2021). In comparison, the first papers using these invasion terms appear in 1986, and now total 27,100. Although the increasing usage of physiology in these papers is encouraging (figure 2a), the proportion of invasion papers using physiology remains low (less than 2%; figure 2b) and suggests that this field it still being underused.

Invasive species foster rich collaboration among physiologists, ecologists, evolutionary biologists, and land managers, with great potential for growth and discovery. Biological invasions are natural experiments that have expanded our understanding of ecological and evolutionary theory, including theoretical predictions of range limits, community assembly, and ecological genetics (Lodge 1993, Davis and Guy 2001, Sax et al. 2005, Pearson et al. 2018). Similarly, invasive species provide robust tests of the assumptions underlying mechanistic models of population dynamics developed from laboratory studies (Kearney et al. 2008). Finally, owing to their economic and ecological consequences, biological invasions can be crisis events (*sensu* Pennington et al. 2013) that catalyze interdisciplinary collaborations. By keeping invasive species in mind, physiologists can build their experiments to include abiotic variables needed for modeling response curves (box 2). We propose the following framework to help guide researchers toward the necessary types of data: justifying physiological traits of interest, determining ecologically appropriate time frames, identifying relevant abiotic variables, designing experimental treatments that capture covariation between abiotic variables, measuring physiological responses to these abiotic variables, and fitting statistical models to the data. Full details are provided in figure 3.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Box 2. Using physiological data to model biological invasions.

Making physiological data more valuable for modeling response curves can be initiated in the experimental design stage (figure 3). Response curves are multivariate landscapes that capture the interactions among variables. Although most abiotic variables are continuous in magnitude, physiologists usually design experiments with discrete levels. This approach reduces the resources needed for an experiment (e.g., the number of incubators or water baths needed to control temperature) but may fail to capture a complex, nonlinear effect of a continuous variable on a physiological process. An alternative approach, which maximizes the power to describe a nonlinear response, is to assign a random treatment level to each replicate in the experiment. For example, consider three experiments designed to measure the relationship between body temperature and physiological performance:

- measure the performance of a number, *N*, of animals divided among a few temperatures, evenly spaced throughout the range (e.g., Niehaus et al. 2012);
- measure the performance of *N* animals divided among a few temperatures, strategically spaced to capture nonlinear portions of the range (e.g., Cooper et al. 2010); or
- measure the performance of *N* animals, each assigned to a randomly selected temperature in the range (e.g., James et al. 2015).

The first design reflects a common approach to physiological experiments but offers the least power to describe a nonlinear response. The second design prioritizes data in the portion of the response with the greatest nonlinearity, more accurately conveying the curvature of the response; however, this design is limited if researchers mistakenly cluster temperatures in the approximately linear part of the curve. The third option—a randomized, continuous design—affords the greatest power to accurately model an unknown nonlinear response (Steury et al. 2002, Cottingham et al. 2005, Steury and Murray 2005, Lazic 2008) but requires the most effort to establish and maintain treatment levels. Favoring a randomized continuous design when resources permit with this type of experiment generates data with the greatest value for modeling response curves. More elaborate designs can quantify how response curves vary among life stages or genotypes and across invasion stages to further increase the ability to predict population dynamics under natural conditions (Sinclair et al. 2016).

Many statistical tools exist for fitting functions to data generated by a randomized, continuous design (see Zuur et al. 2009). Generalized linear mixed modeling offers the greatest flexibility, because one can choose the most appropriate distribution for the stochastic component of the model (Bolker et al. 2009). A nonlinear response can be modeled either by including a quadratic term in the generalized linear model or by fitting a nonlinear model (Peek et al. 2002) or a generalized additive model (Pedersen et al. 2019, Ravindra et al. 2019). If the data have a nested structure, such as when the same dependent variable is measured for an individual at multiple times or under multiple conditions, a mixed model enables one to include a random effect on the intercept or a slope. Finally, model selection or model averaging can be used to estimate the most likely values of parameters with greater accuracy (Burnham and Anderson 2002, Johnson and Omland 2004, Symonds and Moussalli 2011), especially when an experiment was used to break any covariation among independent variables (Cade 2015, Dormann et al. 2018). The parameters estimated from these analytical approaches, along with estimates of uncertainty, are essential for modeling or simulating ecological processes such as a biological invasion (Canham et al. 2003, Gotelli and Ellison 2004).

Physiological research on local adaptation and phenotypic plasticity is needed to understand how fitness depends on particular traits across invasion stages (figure 1). Understanding where we should expect strong phenotypic variation or phenotypic plasticity narrows the circumstances in which a trait-based approach can predict invasions (box 1). The fundamental niche—and, therefore, the potential range of a species—depends on demographic processes that determine whether a population will persist in an area (Hutchinson 1957). The theory in this area of ecology is strong but often lacks an explicit link to physiology, despite species distribution models being built on climate data, which has strong links to a species's thermal physiology (Kearney and Porter 2009, Sinclair et al. 2016, Angilletta et al. 2019). A key contribution of physiologists to invasion ecology would be to link traits such as physiological performance to fitness and the potential for population growth, as was determined by rates of survival and fecundity (box 2).

Scaling physiological responses to demographic outcomes

Demographic population models and multivariate statistical models (general additive models, general linear models, maximum entropy, random forests) are extensively used by invasion scientists to determine which introduced populations will persist and spread (Elith and Leathwick 2009). These models often assume that demographic rates result from physiological responses to the environment (for a discussion, see Gallien et al. 2010). This assumption can be misleading for many reasons (Elith and Leathwick 2009), but the one most relevant in the present article is static trait values (box 1). To support a mechanistic understanding of the demographic dynamics of invasive species over space and time, one must relate availability of energy and resources in nonnative organisms to rates of survival and fecundity, the demographic features that determine population dynamics (Griffith and Loik 2010). Although several biotic and abiotic ecological factors can affect population dynamics, physiological traits constrain the rates of survival and fecundity

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

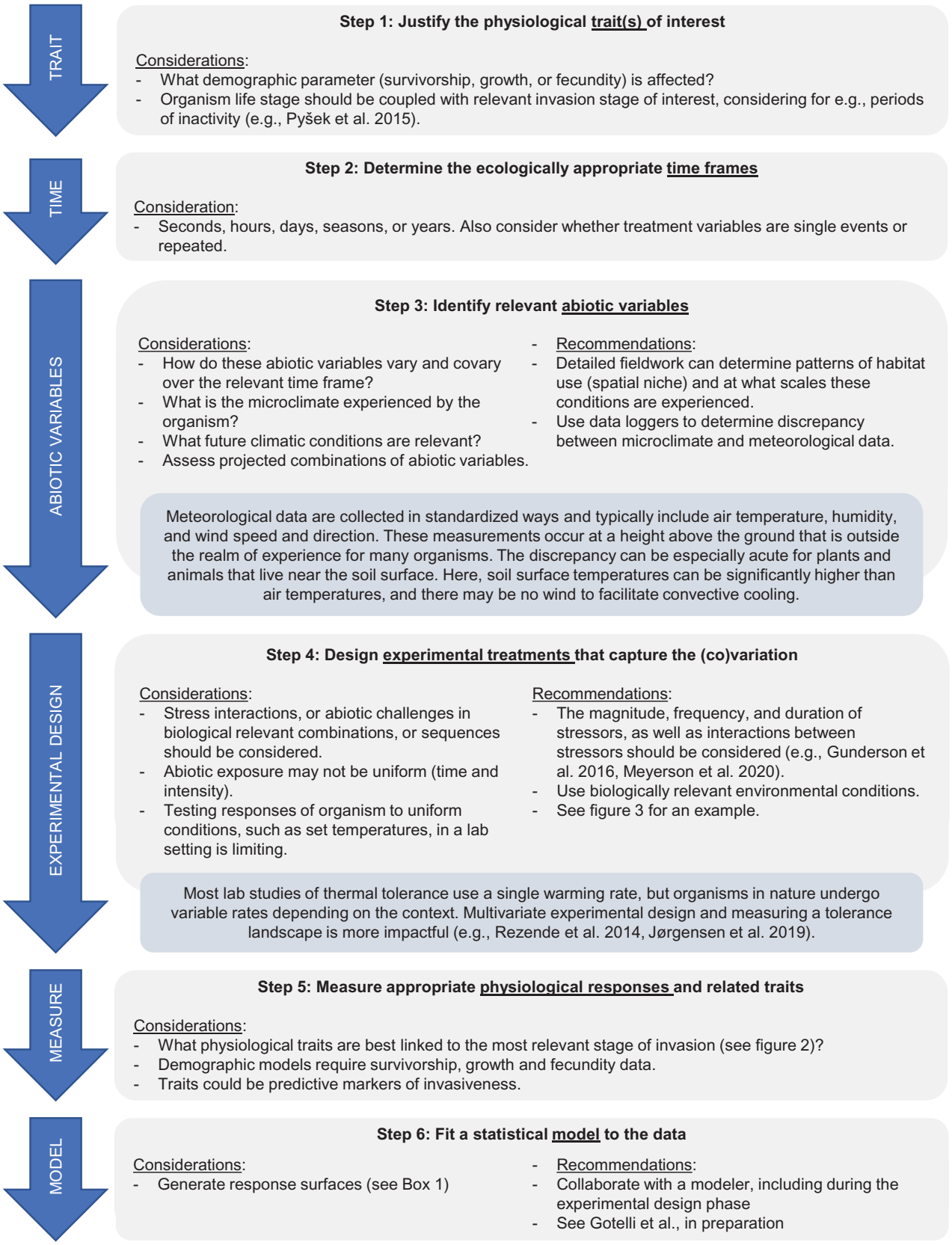

Figure 3. The framework for designing experiments to quantify any physiological function related to demography. The steps are designed to yield models of response surfaces that capture ecologically relevant variation and enable stronger predictions of invasions.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

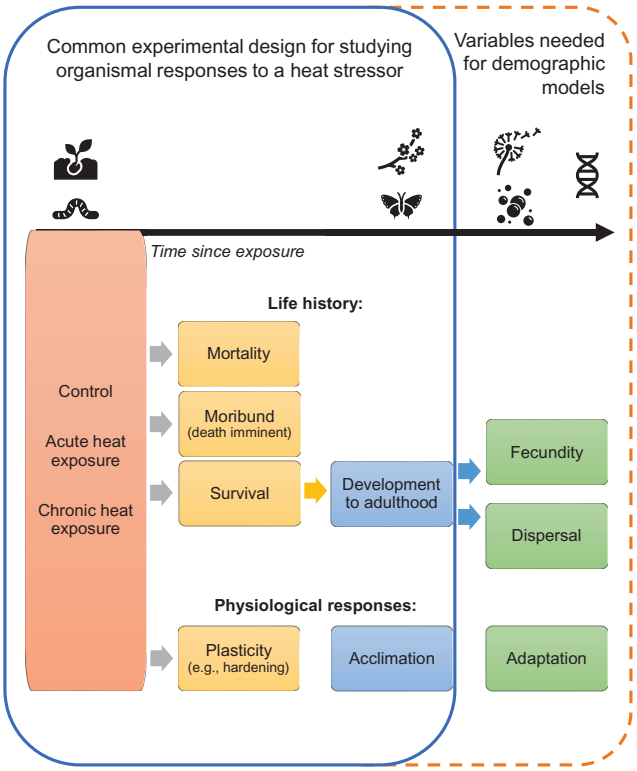

Figure 4. Although life history traits and physiological responses are important for understanding how an abiotic stress affects an organism, invasion science also requires knowledge of development to adulthood (reproductive maturity), fecundity, dispersal, and adaptation to identify which species have invasive potential. The solid box shows a common experimental design used by physiologists to study organismal responses to a stressor in the lab (e.g., short-term responses after heat exposure in an immature life stage). The stippled box shows an extension of this design to include variables essential for demographic modeling, including other life stages.

for an organism (Kearney and Porter 2009, Angilletta et al. 2019).

One factor limiting our ability to link physiological responses more broadly, beyond the well-studied organisms such as lionfish and sea lamprey (see the introduction), to demographic impacts is a lack of relevant knowledge about the physiological responses of invasive organisms to environmental conditions. Common research foci of ecological physiologists are pertinent to invasion science, such as thermal limits (Verberk et al. 2016, MacMillan 2019) and stress responses (e.g., Boardman et al. 2016; for a review, see Kassahn et al. 2009). However, physiologists often examine these topics from a different perspective when not directly studying nonnative species (see figure 4), leading them to ask questions better answered with lab-based approaches. Although they are valuable in their own fields, the treatments in physiological experiments deviate from the field conditions that are more pertinent to invasion science (e.g., using implausible temperature ranges, constant temperatures, or extreme conditions not experienced in nature; e.g., Angilletta et al. 2000; and see discussions relating to measuring thermal tolerance in ectotherms; Terblanche et al. 2011). In addition, physiological experiments are often ended before one could observe the demographic variables needed for modeling potential invasions (figure 4; e.g., mortality was observed but fecundity was not by Boardman et al. 2012). Although measuring these demographic variables was not central to the research question investigated, with invasion science in mind, these experiments could have been modified to include variables essential for demographic modeling (see the stippled block in figure 4), allowing future invasion scientists to repurpose the data when needed. Some plant physiologists have done this, and their work offers examples for animal physiologists to follow (e.g., Miller and Gorchov 2004, Concilio et al. 2013).

Thermal tolerance has been well studied by physiologists and invasion scientists alike. Comparative studies of thermal tolerance and acclimation responses of native and invasive species (e.g., ladybird beetles, Boher et al. 2018; frogs, Cortes et al. 2016; and weeds, Parker et al. 2003) or across native and invasive ranges of the same species (e.g., European green crab *Carcinus maenas*, Tepolt and Somero 2014; cheatgrass *Bromus tectorum*, Griffith et al. 2014) are common. The focus on temperature for predicting the ranges of invasive species statistically dates back to climographs (Cook 1925, 1931). Because thermal tolerance is key for determining species distributions and sets a hard limit for survival, measures of thermal tolerance are often incorporated into demographic models or into statistical models that assume an underlying demographic response of individuals to temperature (e.g., Crozier and Dwyer 2006, Laeseke et al. 2020, Tremblay et al. 2020). Because temperature can easily be manipulated in the lab, thermal traits are well suited to lab experiments, making this trait useful for connecting physiology to invasion success. However, physiological response surfaces (reaction norms) are needed to infer demographic responses (Rezende et al. 2014; discussed in box 2). Performing a full suite of both static and dynamic thermal measurements to obtain this type of response variable can be time consuming and require large samples. For example, for 11 *Drosophila* species, critical thermal maximum was measured as heat tolerance knockdown time at multiple temperatures (static) and compared with tolerance from gradual warming at different ramping rates (dynamic) to study correlations between heat tolerance measures and environmental conditions in the origins of each species (Jørgensen et al. 2019).

Although many physiological traits can be measured in the field (e.g., gill beat rate to measure respiration, reflex assessment tests), other physiological traits can be time or labor intensive to measure or very difficult to capture in the study organism, so many researchers focus on traits of model species, such as *Arabidopsis thaliana* or *Drosophila*

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

melanogaster, for which methods are well defined. The mean values for these surrogate species are often applied to closely related invasive species, for which data do not exist (e.g., Williams et al. 2016). In some cases, traits are conserved between phylogenetically close species (e.g., Luong et al. 2021). However, recent work indicates that closely related or ecologically similar species often have very different demographic rates; therefore, one should not assume that trait values for one species are suitable proxies for those of another (Che-Castaldo et al. 2018). Invasion scientists should be cautious when estimating parameter values from data for ecologically or phylogenetically related species (see Bolnick et al. 2011 and Des Roches et al. 2018 for discussions on intraspecific variation). When forced to estimate parameter values from data for other species, one can perform a sensitivity analysis to determine which parameters have the biggest impact on population dynamics. Such an analysis would point to future experiments needed to confirm the values for the species of concern. Invasion scientists and physiologists should collaborate to conduct targeted investigations on a broader diversity of species, not just well-studied model systems (e.g., *Phragmites australis*, *Arabidopsis thaliana*; Williams et al. 2016; for discussions, see Pyšek et al. 2008, Kueffer et al. 2013, Gundale et al. 2014, and Meyerson et al. 2016b). Investigating a variety of taxa can yield other benefits, such as shedding light on how physiological traits evolved and the origin and maintenance of interspecific variation.

Physiologists can contribute to this effort by designing lab experiments to yield fitness values that can be incorporated into demographic and statistical invasion models. In particular, data relating to reaction norms, tolerance, plasticity, hysteresis, and performance are essential (see below). Physiologists can also contribute by measuring the physiology of organisms in their native and nonnative environments to understand physiological mechanisms that enable these organisms to survive under typical conditions and novel conditions, respectively. Similarly, plant physiologists can evaluate tolerance of stress (e.g., drought, flooding, salinity, plasticity and fitness of invaders at range edges), paying particular attention to different cytotypes, because many invasive plants are polyploids with small genomes (Suda et al. 2015).

Models to predict physiological processes

To model the potential for a species to persist in an environment, biologists must specify relationships between abiotic variables and the physiological processes that determine an organism's survival, development, growth, and reproduction (box 2; Kearney and Porter 2009, Peterson et al. 2015, Angilletta et al. 2019). These relationships, called *response curves*, are multivariate landscapes that capture the interactions among variables such as temperature, moisture, light, and food (e.g., Brett 1971). In the case of invasive species, understanding the multivariate landscape encompassing abiotic conditions, physiological processes, and demographic outcomes can be particularly useful for modeling how they may respond to conditions in their nonnative range, including future climate change (Beaury et al. 2020). For highly nonlinear response curves, one must have sufficient data to characterize the response accurately over the ranges of abiotic conditions in the native region and the invaded region. Without such data, one must take the risky approach of extrapolating beyond the fitted bounds of the function.

Abiotic interactions. Multivariate response curves will account for important interactions between abiotic variables. Numerous abiotic and biotic conditions may affect invasiveness. These multiple potentially covarying and interacting factors make predicting invasions challenging; however, understanding the physiological responses to combinations of abiotic and biotic variables may yield better predictions. Two commonly studied interacting abiotic factors influencing invasions are temperature and salinity. The Indo-Pacific mytilid *Brachidontes pharaonis* tolerates high salinity in its native range. This species managed to colonize habitats with high salinity in the Western Mediterranean through the Suez Canal before spreading west throughout the Mediterranean, outcompeting indigenous bivalves. Measuring physiological variables, including respiration rate and scope for growth, in response to a combination of temperatures and salinities, Sarà and colleagues (2008) showed that *B. pharaonis* can survive and reproduce in a wide range of conditions, facilitating its westward spread. Likewise, interactions between salinity and temperature affect germination rate of the desert plant *Prosopis juliflora*, which invaded the United Arab Emirates (El-Keblawy and Al-Rawai 2005). In this example, the germination rate in seeds treated at low salinities was highest at high temperatures (40 °C); germination rate at intermediate temperature (25°C) was less affected by salinity. The effects of these conditions can be complicated to study and include in models, because abiotic factors can interact in unpredictable ways. Perhaps for this reason, interactions between abiotic factors are often neglected in studies of the causes of biological invasions or treated implicitly in multivariate models.

Biotic interactions. Finally, the presence or absence of other species will shape response curves of invasive species through biotic interactions. An interesting case is presented by the potentially overlapping ranges of the aquatic plant *Trapa natans* (figure 5a), introduced to North America in the 1800s and now widely distributed, and of *Trapa bispinosa*, very recently introduced to the Potomac River Watershed in Virginia, in the United States (Dodd et al. 2021). Although limited data suggest that *T. bispinosa* may be a better competitor than *T. natans* (Dodd et al. 2021), the physiological tolerances and competitive ability of *T. bispinosa* across a range of thermal conditions have not been explored. How physiological limits and tolerances affect competitive ability in closely related invaders is an underexplored question. One should also consider the biotic

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

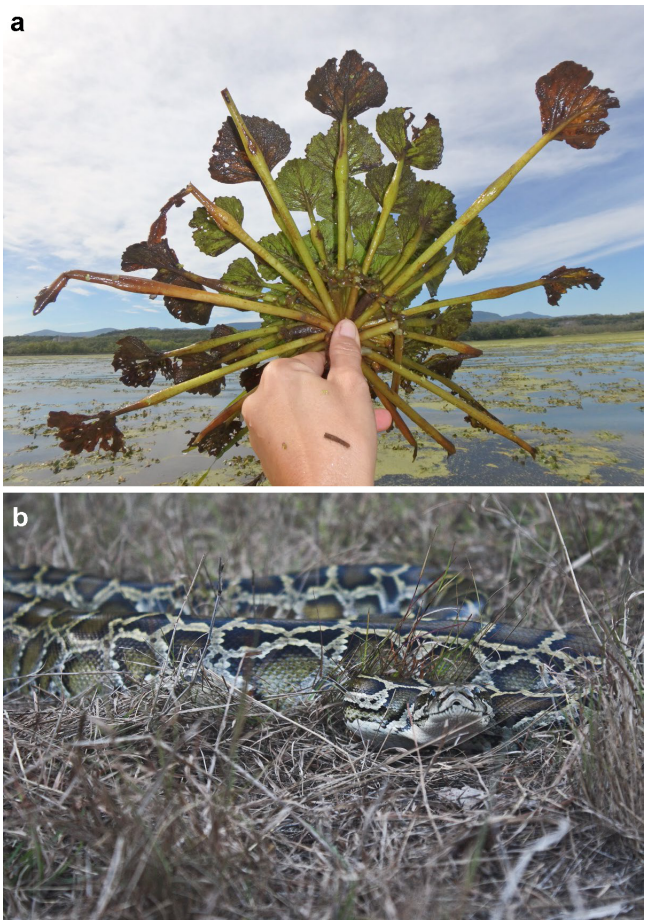

Figure 5. (a) *Trapa natans* ***(water chestnut or water caltrop) is a floating aquatic species native to Europe and Asia first introduced to North America in the 1800s. (b)*** *Python bivittatus* ***(the Burmese python) is native to southeast Asia and has become established in South Florida, in the United States, including Everglades National Park, after the release of pet pythons, and escape from breeding facility during Hurricane Andrew. Photographs: Lynde Dodd (a) and Kodiak Hengstebeck (b).***

factors that may affect organisms or interact with their stress responses and should determine whether these factors play a role in invasion (Suzuki et al. 2014, Le Roux et al. 2020). Indirect biotic effects are defined as "how one species alters the effect that another species has on a third" (White et al. 2006). These biotic interactions commonly pertain to apparent competition, indirect mutualism or commensalism, exploitative competition, and trophic cascades (for a review, see White et al. 2006; e.g., the effects of Burmese pythons on nonprey species in the Everglades; figure 5b; Willson 2017). More broadly, these factors could include bacterial or viral infections, immune responses, microbial environment, interspecies competition, and herbivory (e.g., Claunch et al. 2021; see Dunn et al. 2012 for a review of role of parasites in invasions and Schulz et al. 2019 for a review on antagonistic interactions between native and nonnative species).

Overcoming barriers to integration of physiology and invasion science

Despite the potential gains from more fully integrating physiology and invasion science, several barriers limit the use of existing physiological data in invasion science. These barriers can include ecologically meaningless lab conditions, the routine use of constant lab conditions, and a lack of scope for an organism's behavioral responses. However, each of these barriers could potentially be overcome by modifying typical laboratory experimental designs, applying new technologies, or embracing the messiness of the field. First, physiological trait data are often collected via lab experiments. Laboratory conditions may poorly mimic the conditions that organisms experience in the field. For example, lab experiments usually involve constant abiotic factors, no species interactions, and unrealistic levels or durations of treatments (see the earlier discussion and figure 4). As a result, the value of the data for modeling invasions can be limited. Despite these barriers, lab experiments have the advantage of including abiotic conditions that organisms might not experience currently but could face in the future. These types of experiments can also be completed in the field—for instance, by conducting reciprocal transplants across bioclimatic zones (reviewed by Sexton et al. 2009, Hargreaves et al. 2014) or by treatments simulating alternate temperature or precipitation regimes (e.g., Knapp et al. 2017, Zettlemoyer et al. 2019). Lab studies do not pose ethical issues associated with releasing potential invasives in the field. Therefore, both lab and field approaches can provide valuable insights for invasion science, especially if the lab experiments are designed to be as ecologically meaningful as possible and if the field experiments are conducted ethically.

Second, experiments often limit the organism's suite of tactics for responding to the manipulation of interest (for discussions of lab and field experiments, see Calisi and Bentley 2009). For example, research on the chemical control of insects routinely includes toxicity tests performed in the laboratory. However, in field situations, insect behavior (e.g., moving to the underside of leaves or reducing feeding) can limit the efficacy of the treatment, leaving the lab-based research with reduced applicability in limiting the spread of or damage by an invasive species (Denholm and Rowland 1992, Hoy et al. 1998). For a thorough review of the behavioral changes caused by biological invasions across taxonomic groups, see Ruland and Jeschke (2020). Once again, we are not advocating the uncontrolled release of invasives in field tests. However, thoughtful experimental design that accounts for these responses will inform invasion science (figure 3).

Third, organisms in the lab are often exposed to constant conditions or smooth transitions between conditions. By contrast, organisms in nature experience cyclically, stochastically fluctuating, or short-lived extreme conditions. Each of these factors can be incorporated into physiological research by increasing the ecological realism of experimental conditions or even taking the experiment into the field. For

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

example, designing laboratory experiments with fluctuating parameters that represent daily and seasonal deviations from the expected values will improve relevance of data to natural conditions (e.g., Niehaus et al. 2012, Atamian and Harmer 2016, Grinevich et al. 2019), as well as applications to invasions. Data on how fluctuating or extreme conditions influence traits related to fecundity are especially relevant for invasions (e.g., Marshall and Sinclair 2018). Controlled environments such as incubators and glasshouses have benefited from recent technological developments—integrated automation, programming, measurement, control systems with smart sensors—that allow for even finer tuning of conditions and simulation of field conditions (e.g., Chavan et al. 2020, Tiatragul et al. 2020). However, the added complexity of the dynamic variables and expense of creating these environments may restrict their adoption.

Future directions

To fully leverage physiological information to inform invasion science, new collaborative teams must be created to share data and expertise. Funded workshops, such as The Rules of Life Underlying Biological Invasions (Meyerson et al. 2019), can facilitate building these collaborations and diversify research networks of invasion scientists. The composition of these teams will depend on the invasive organism itself and its impacts but could include physiologists, ecologists, evolutionary biologists, and land managers. Scientists involved in policy, conservation, and taxonomy may also be valuable. Broader impacts will accrue from the multidisciplinary training opportunities that will develop as new collaborations, databases, and networks evolve in this effort between laboratory physiologists and field ecologists. We see opportunities to provide benefits for all participants, as this approach creates fundable scientific endeavors as the NSF and other funding agencies fund integrative and predictive research.

Even before all funding agencies move fully to require publicly available data for each publication, physiologists should ensure that their data are publicly available and easily accessible, with relevant metadata and informative tags. Data sharing will greatly extend the significance of their data beyond their original use (Christensen et al. 2019, Soeharjono and Roche 2021). When new invasive species emerge, preexisting data may facilitate quicker responses—if the data can be found and accessed. One way to facilitate this access would be by developing trait databases (e.g., Madin et al. 2016, Brun et al. 2017, Liu et al. 2017, Degen et al. 2018). Many existing and emerging technologies and networks can help facilitate integrating physiological data into invasion science. Museums, field facilities with long histories (e.g., Rocky Mountain Biological Laboratory), and regional (e.g., University of California Natural Reserves) or national (e.g., the United States Long Term Ecological Research Network) networks can provide long-term physiological proxy data from tree rings, pressed botanical specimens, pinned insects, and animal skins (e.g., DeLeo et al. 2020). NEON (the National Ecological Observatory Network) is a continental-scale observatory of 81 coordinated monitoring sites across North America (Loescher et al. 2017) that provides open data to monitor changes in terrestrial and aquatic ecosystems. Although NEON does not directly collect physiological data, it does collect data directly relevant to physiological research (e.g., weather and climate data, microclimate data, plant phenology, sampling on sentinel taxa; www.neonscience.org/data-collection). These resources should be mined for new insights into emergent properties of the physiology of invasive organisms (AIBS 2004). The ecological sciences are undergoing a transformation driven by the recent increase in massive, rapid, and diverse sources of information and methods to analyze that information. There has never been a better time for compiling and querying massive amounts of data. Big, rapid, and diverse data sets are opening new avenues of research and should facilitate exciting new discoveries at the crossroads of physiology and invasion science.

Although physiology is increasingly mentioned in invasion papers, it is still underrepresented in invasion science overall. In the present article, we have provided evidence for the value in including physiologists in collaborations to answer questions relating to invasion science and provided a framework of how to proceed in this direction. Data for demography models can be collected in the lab or under very controlled seminatural field conditions without risk of accidental introduction of invasives. To further increase the value of this integrated approach, physiologists can collect data under simulated future climate change conditions or use biogeographic approach that includes studying populations the field in different abiotic conditions paired with greenhouse experiments that study the same populations in a common garden. This intentional, invasion-focused collection of physiological data will facilitate improved demographic models to inform invasion science. As environmental change intensifies, additional tools will be needed to limit the impacts of invasions.

Acknowledgments

Special thanks to Lynde Dodd and Kodiak Hengstebeck for providing the photographs used in figure 5. Thanks also to the editor and two reviewers whose comments greatly improved the manuscript.

This work was supported by National Science Foundation grant no. DEB ROL 183968, awarded to LAM, JLL, and DS.

References cited

[AIBS] American Institute of Biological Sciences. 2004. Designing NEON Initiatives for Invasive Species: Report from a NEON Science Workshop. AIBS.

Angilletta MJJr, Winters SR, Dunham AE. 2000. Thermal effects on the energetics of lizard embryos: Implications for hatching phenotypes. Ecology 81: 2957–2968.

Angilletta MJ, Sears MW, Levy O, Youngblood JP, Vandenbrooks JM. 2019. Fundamental flaws with the fundamental niche. Integrative and Comparative Biology 59: 1038–1048.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Atamian HS, Harmer SL. 2016. Circadian regulation of hormone signaling and plant physiology. Plant Molecular Biology 91: 691–702.
Atwater DZ, Ervine C, Barney JN. 2018. Climatic niche shifts are common in introduced plants. Nature Ecology and Evolution 2: 34–43.
Beaury EM, Fusco EJ, Jackson MR, Laginhas BB, Morelli TL, Allen JM, Pasquarella VJ, Bradley BA. 2020. Incorporating climate change into invasive species management: Insights from managers. Biological Invasions 22: 233–252.
Behrens JW, Van Deurs M, Christensen EAF. 2017. Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. PLOS ONE 12: e0176038.
Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F. 2013. Will climate change promote future invasions? Global Change Biology 19: 3740–3748.
Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339.
Blackburn TM, Bellard C, Ricciardi A. 2019. Alien versus native species as drivers of recent extinctions. Frontiers in Ecology and the Environment 17: 203–207.
Blossey B, Notzold R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. Journal of Ecology 83: 887–889.
Boardman L, Grout TG, Terblanche JS. 2012. False codling moth *Thaumatotibialeucotreta* (Lepidoptera, Tortricidae) larvae are chill-susceptible. Insect Science 19: 315–328.
Boardman L, Sørensen JG, Koštál V, Šimek P, Terblanche JS. 2016. Cold tolerance is unaffected by oxygen availability despite changes in anaerobic metabolism. Scientific Reports 6: 32856.
Boher F, Jaksic FM, Martel SI, Orellana MJ, Bozinovic F. 2018. Does thermal physiology explain the ecological and evolutionary success of invasive species? Lessons from ladybird beetles. Evolutionary Ecology Research 19: 243–255.
Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JS. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127–135.
Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26: 183–192.
Brett JR. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchusnerkd*). American Zoologist 11: 99–113.
Briski E, Chan FT, Macisaac HJ, Bailey SA. 2014. A conceptual model of community dynamics during the transport stage of the invasion process: A case study of ships' ballast. Diversity and Distributions 20: 236–244.
Brun P, Payne MR, Kiørboe T. 2017. A trait database for marine copepods. Earth System Science Data 9: 99–113.
Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach 2nd ed. Springer.
Cade BS. 2015. Model averaging and muddled multimodel inferences. Ecology 96: 2370–2382.
Calisi RM, Bentley GE. 2009. Lab and field experiments: Are they the same animal? Hormones and Behavior 56: 1–10.
Cameron EK, Vilà M, Cabeza M. 2016. Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Global Ecology and Biogeography 25: 596–606.
Canham C, Cole J, Lauenroth W. 2003. Models in Ecosystem Science. Princeton University Press.
Capellini I, Baker J, Allen WL, Street SE, Venditti C. 2015. The role of life history traits in mammalian invasion success. Ecology Letters 18: 1099–1107.
Card DC, et al. 2018. Novel ecological and climatic conditions drive rapid adaptation in invasive Florida Burmese pythons. Molecular Ecology 27: 4744–4757.
Catford JA, Jansson R, Nilsson C. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22–40.
Chavan SG, et al. 2020. Light-limited photosynthesis under energy-saving film decreases eggplant yield. Food and Energy Security 9: e245.
Che-Castaldo J, Che-Castaldo C, Neel MC. 2018. Predictability of demographic rates based on phylogeny and biological similarity. Conservation Biology 32: 1290–1300.
Chen C, Condon CH, Boardman L, Meagher RL, Jeffers LA, Beam A, Bailey WD, Hahn DA. 2020. Critical PO2 as a diagnostic biomarker for the effects of low-oxygen modified and controlled atmospheres on phytosanitary irradiation treatments in the cabbage looper *Trichoplusiani* (Hübner). Pest Management Science 76: 2333–2341.
Chown SL, Gaston KJ. 2008. Macrophysiology for a changing world. Proceedings of the Royal Society B 275: 1469–1478.
Christensen G, Dafoe A, Miguel E, Moore DA, Rose AK. 2019. A study of the impact of data sharing on article citations using journal policies as a natural experiment. PLOS ONE 14: e0225883.
Claunch N, Moore I, Waye H, Schoenle L, Oakey SJ, Reed RN, Romagosa C. 2021. Understanding metrics of stress in the context of invasion history: The case of the brown treesnake (*Boigairregularis*). Conservation Physiology 9: coab008.
Colautti RI, Barrett SCH. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. Science 342: 364–366.
Concilio AL, Loik ME, Belnap J. 2013. Global change effects on *Bromustectorum* l. (Poaceae) at its high-elevation range margin. Global Change Biology 19: 161–172.
Cook WC. 1925. The distribution of the alfalfa weevil (*Phytonomusposticus* Gyll.). A study in physical ecology. Journal of Agricultural Research 30: 479–491.
Cook WC. 1931. Notes on predicting the probable future distribution of introduced insects. Ecology 12: 245–247.
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: cot001.
Cooke SJ, et al. 2020. Reframing conservation physiology to be more inclusive, integrative, relevant and forward-looking: Reflections and a horizon scan. Conservation Physiology 8: coaa016.
Cooper BS, Czarnoleski M, Angilletta Jr MJ. 2010. Acclimation of thermal physiology in natural populations of Drosophila melanogaster: A test of an optimality model. Journal of Evolutionary Biology 23: 2346–2355.
Cortes PA, Puschel H, Acuña P, Bartheld JL, Bozinovic F. 2016. Thermal ecological physiology of native and invasive frog species: Do invaders perform better? Conservation Physiology 4: cow056.
Cottingham KL, Lennon JT, Brown BL. 2005. Knowing when to draw the line: Designing more informative ecological experiments. Frontiers in Ecology and the Environment 3: 145–152.
Cronin JT, Bhattarai GP, Allen WJ, Meyerson LA. 2015. Biogeography of a plant invasion: Plant–herbivore interactions. Ecology 96: 1115–1127.
Crozier L, Dwyer G. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. American Naturalist 167: 853–866.
Crystal-Ornelas R, Lockwood JL. 2020. The "known unknowns" of invasive species impact measurement. Biological Invasions 22: 1513–1525.
Davis LT, Guy PL. 2001. Introduced plant viruses and the invasion of a native grass flora. Biological Invasions 3: 89–95.
Degen R, et al. 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. Ecological Indicators 91: 722–736.
DeLeo VL, Menge DNL, Hanks EM, Juenger TE, Lasky JR. 2020. Effects of two centuries of global environmental variation on phenology and physiology of *Arabidopsisthaliana*. Global Change Biology 26: 523–538.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Denholm I, Rowland MW. 1992. Tactics for managing pesticide resistance in arthropods: Theory and practice. Annual Review of Entomology 37: 91–112.

Des Roches S, Post DM, Turley NE, Bailey JK, Hendry AP, Kinnison MT, Schweitzer JA, Palkovacs EP. 2018. The ecological importance of intraspecific variation. Nature Ecology and Evolution 2: 57–64.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105: 6668–6672.

di Castri F. 1989. History of biological invasions with special emphasis on the old world. Pages 1–30 in Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M, eds. Biological Invasions. A Global Perspective. Wiley.

Dodd LL, Harms NE, Schad AN. 2021. Reciprocal competitive effects of congeneric invaders, *Trapanatans* l. and *Trapabispinosa* roxb. var. *iinumai* Nakano, in established freshwater plant cultures. Aquatic Botany 174: 103419.

Dormann CF, et al. 2018. Model averaging in ecology: A review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecological Monographs 88: 485–504.

Duggan IC, Rixon CAM, MacIsaac HJ. 2006. Popularity and propagule pressure: Determinants of introduction and establishment of aquarium fish. Biological Invasions 8: 377–382.

Dunn AM, et al. 2012. Indirect effects of parasites in invasions. Functional Ecology 26: 1262–1274.

Early R, et al. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. Nature Communications 7: 12485.

Elith J, Leathwick JR. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40: 677–697.

El-Keblawy A, Al-Rawai A. 2005. Effects of salinity, temperature and light on germination of invasive *Prosopisjuliflora* (Sw.) D.C. Journal of Arid Environments 61: 555–565.

Eller F, et al. 2017. Cosmopolitan species as models for ecophysiological responses to global change: The common reed *Phragmitesaustralis*. Frontiers in Plant Science 8: 01833.

Enders M, et al. 2020. A conceptual map of invasion biology: Integrating hypotheses into a consensus network. Global Ecology and Biogeography 29: 978–991.

Engel K, Tollrian R, Jeschke JM. 2011. Integrating biological invasions, climate change and phenotypic plasticity. Communicative and Integrative Biology 4: 247–250.

Essl F, et al. 2015. Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769–782.

Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W. 2010. Predicting potential distributions of invasive species: Where to go from here? Diversity and Distributions 16: 331–342.

Gotelli N, Ellison A. 2004. Primer of Ecological Statistics. Sinaeur.

Griffith AB, Loik ME. 2010. Effects of climate and snow depth on *Bromustectorum* population dynamics at high elevation. Oecologia 164: 821–832.

Griffith AB, Andonian K, Weiss CP, Loik ME. 2014. Variation in phenotypic plasticity for native and invasive populations of *Bromustectorum*. Biological Invasions 16: 2627–2638.

Grinevich DO, Desai JS, Stroup KP, Duan J, Slabaugh E, Doherty CJ. 2019. Novel transcriptional responses to heat revealed by turning up the heat at night. Plant Molecular Biology 101: 1–19.

Gundale MJ, Pauchard A, Langdon B, Peltzer DA, Maxwell BD, Nuñez MA. 2014. Can model species be used to advance the field of invasion ecology? Biological Invasions 16: 591–607.

Gunderson AR, Armstrong EJ, Stillman JH. 2016. Multiple stressors in a changing world: The need for an improved perspective on physiological responses to the dynamic marine environment. Annual Review of Marine Science. doi:10.1146/annurev-marine-122414-033953

Hallegraeff GM, Valentine JP, Marshall JA, Bolch CJ. 1997. Temperature tolerances of toxic dinoflagellate cysts: Application to the treatment of ships' ballast water. Aquatic Ecology 31: 47–52.

Hargreaves AL, Samis KE, Eckert CG. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. American Naturalist 183: 157–173.

Hasenei A, Kerstetter DW, Horodysky AZ, Brill RW. 2020. Physiological limits to inshore invasion of Indo-Pacific lionfish (*Pterois* spp.): Insights from the functional characteristics of their visual system and hypoxia tolerance. Biological Invasions 22: 2079–2097.

Higgins SI, Richardson DM. 2014. Invasive plants have broader physiological niches. Proceedings of the National Academy of Sciences 111: 10610–10614.

Hodgins KA, Bock DG, Rieseberg LH. 2018. Trait evolution in invasive species. Annual Plant Reviews Online 1: 1–37.

Holway DA, Suarez A V. 2006. Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion. Biological Conservation 127: 319–326.

Hoy CW, Head GP, Hall FR. 1998. Spatial heterogeneity and insect adaptation to toxins. Annual Review of Entomology 43: 571–594.

Huey RB, Kingsolver JG. 1993. Evolution of resistance to high temperature in ectotherms. The American Naturalist 142: S21–S46.

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287: 308–309.

Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427.

James RS, Tallis J, Angilletta Jr MJ. 2015. Regional thermal specialisation in a mammal: Temperature affects power output of core muscle more than that of peripheral muscle in adult mice (Mus musculus). Journal of Comparative Physiology B. doi:10.1007/s00360-014-0872-6

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101–108.

Jørgensen LB, Malte H, Overgaard J. 2019. How to assess *Drosophila* heat tolerance: Unifying static and dynamic tolerance assays to predict heat distribution limits. Functional Ecology 33: 629–642.

Jud ZR, Nichols PK, Layman CA. 2015. Broad salinity tolerance in the invasive lionfish *Pterois* spp. may facilitate estuarine colonization. Environmental Biology of Fishes 98: 135–143.

Karsiotis SI, Pierce LR, Brown JE, Stepien CA. 2012. Salinity tolerance of the invasive round goby: Experimental implications for seawater ballast exchange and spread to North American estuaries. Journal of Great Lakes Research 38: 121–128.

Kassahn KS, Crozier RH, Pörtner HO, Caley MJ. 2009. Animal performance and stress: Responses and tolerance limits at different levels of biological organisation. Biological Reviews 84: 277–292.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17: 164–170.

Kearney M, Porter W. 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334–350.

Kearney M, Phillips BL, Tracy CR, Christian KA, Betts G, Porter WP. 2008. Modelling species distributions without using species distributions: The cane toad in Australia under current and future climates. Ecography 31: 423–434.

Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA. 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: The dengue mosquito *Aedesaegypti* in Australia. Functional Ecology 23: 528–538.

Knapp AK, et al. 2017. Pushing precipitation to the extremes in distributed experiments: Recommendations for simulating wet and dry years. Global Change Biology 23: 1774–1782.

Kueffer C, Pyšek P, Richardson DM. 2013. Integrative invasion science: Model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist 200: 615–633.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Laeseke P, Martínez B, Mansilla A, Bischof K. 2020. Future range dynamics of the red alga *Capreoliaimplexa* in native and invaded regions: Contrasting predictions from species distribution models versus physiological knowledge. Biological Invasions 22: 1339–1352.

Lazic SE. 2008. Why we should use simpler models if the data allow this: Relevance for ANOVA designs in experimental biology. BMC Physiology 8: 1–7.

Lennox R, Choi K, Harrison PM, Paterson JE, Peat TB, Ward TD, Cooke SJ. 2015. Improving science-based invasive species management with physiological knowledge, concepts, and tools. Biological Invasions 17: 2213–2227.

Lenz M, et al. 2018. Heat challenges can enhance population tolerance to thermal stress in mussels: A potential mechanism by which ship transport can increase species invasiveness. Biological Invasions 20: 3107–3122.

Le Roux JJ, Clusella-Trullas S, Mokotjomela TM, Mairal M, Richardson DM, Skein L, Wilson JR, Weyl OLF, Geerts S. 2020. Biotic interactions as mediators of biological invasions: Insights from South Africa. Pages 387–427 in van Wilgen B, Measey J, Richardson D, Wilson J, Zengeya T, eds. Biological Invasions in South Africa, vol. 35. Springer.

Liu C, Comte L, Olden JD. 2017. Heads you win, tails you lose: Life-history traits predict invasion and extinction risk of the world's freshwater fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 27: 773–779.

Lockwood BL, Somero GN. 2011. Invasive and native blue mussels (genus *Mytilus*) on the California coast: The role of physiology in a biological invasion. Journal of Experimental Marine Biology and Ecology 400: 167–174.

Lockwood JL, et al. 2019. When pets become pests: The role of the exotic pet trade in producing invasive vertebrate animals. Frontiers in Ecology and the Environment 17: 323–330.

Lodge DM. 1993. Biological invasions: Lessons for ecology. Trends in Ecology and Evolution 8: 133–136.

Lodge DM, et al. 2016. Risk analysis and bioeconomics of invasive species to inform policy and management. Annual Review of Environment and Resources 41: 453–488.

Loescher HW, Kelly E, Lea R. 2017. National ecological observatory network: Beginnings, programmatic and scientific challenges, and ecological forecasting. Pages 27–52 in Chabbi A, Loescher HW, eds. Terrestrial Ecosystem Research Infrastructures: Challenges and Opportunities. Routledge.

Luong JC, Holl KD, Loik ME. 2021. Leaf traits and phylogeny explain plant survival and community dynamics in response to extreme drought in a restored coastal grassland. Journal of Applied Ecology 58: 1670–1680.

MacMillan HA. 2019. Dissecting cause from consequence: A systematic approach to thermal limits. Journal of Experimental Biology 222: jeb191593.

Madin JS, et al. 2016. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Scientific Data 3: 160017.

Mahoney PJ, Beard KH, Durso AM, Tallian AG, Long AL, Kindermann RJ, Nolan NE, Kinka D, Mohn HE. 2015. Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. Diversity and Distributions 21: 64–74.

Marshall KE, Sinclair BJ. 2018. Repeated freezing induces a trade-off between cryoprotection and egg production in the goldenrod gall fly, *Eurostasolidaginis*. Journal of Experimental Biology 221: jeb177956.

McCarthy AH, Peck LS, Hughes KA, Aldridge DC. 2019. Antarctica: The final frontier for marine biological invasions. Global Change Biology 25: 2221–2241.

Mead A, Carlton JT, Griffiths CL, Rius M. 2011. Revealing the scale of marine bioinvasions in developing regions: A South African re-assessment. Biological Invasions 13: 1991–2008.

Meyerson LA, Cronin JT, Bhattarai GP, Brix H, Lambertini C, Lučanová M, Rinehart S, Suda J, Pyšek P. 2016a. Do ploidy level and nuclear genome size and latitude of origin modify the expression of *Phragmitesaustralis* traits and interactions with herbivores? Biological Invasions 18: 2531–2549.

Meyerson LA, Cronin JT, Pyšek P. 2016b. *Phragmitesaustralis* as a model organism for studying plant invasions. Biological Invasions 18: 2421–2431.

Meyerson LA, Simberloff D, Boardman L, Lockwood JL. 2019. Toward "rules" for studying biological invasions. Bulletin of the Ecological Society of America 100: e01607.

Meyerson LA, Pyšek P, Lučanová M, Wigginton S, Tran C, Cronin JT. 2020. Plant genome size influences stress tolerance of invasive and native plants via plasticity. Ecosphere 11: e03145.

Miller KE, Gorchov DL. 2004. The invasive shrub, *Loniceramaackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139: 359–375.

Niehaus AC, Angilletta MJ, Sears MW, Franklin CE, Wilson RS. 2012. Predicting the physiological performance of ectotherms in fluctuating thermal environments. Journal of Experimental Biology 215: 694–701.

Ochocki BM, Miller TEX. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. Nature Communications 8: 14315.

Parker IM, Rodriguez J, Loik ME. 2003. An evolutionary approach to understanding the biology of invasions: Local adaptation and general-purpose genotypes in the weed *Verbascumthapsus*. Conservation Biology 17: 59–72.

Pearson DE, Ortega YK, Eren Ö, Hierro JL. 2018. Community assembly theory as a framework for biological invasions. Trends in Ecology and Evolution 33: 313–325.

Pedersen EJ, Miller DL, Simpson GL, Ross N. 2019. Hierarchical generalized additive models in ecology: An introduction with mgcv. PeerJ 7: e6876.

Peek MS, Russek-Cohen E, AD Wait, Forseth IN. 2002. Physiological response curve analysis using nonlinear mixed models. Oecologia 132: 175–180.

Pennington DD, Simpson GL, McConnell MS, Fair JM, Baker RJ. 2013. Transdisciplinary research, transformative learning, and transformative science. BioScience 63: 564–573.

Peterson AT, Papeş M, Soberón J. 2015. Mechanistic and correlative models of ecological niches. European Journal of Ecology 1: 28–38.

Piscart C, Kefford BJ, Beisel JN. 2011. Are salinity tolerances of non-native macroinvertebrates in france an indicator of potential for their translocation in a new area? Limnologica 41: 107–112.

Pyron RA, Burbrink FT, Guiher TJ. 2008. Claims of potential expansion throughout the U.S. by invasive python species are contradicted by ecological niche models. PLOS ONE 3: e2931.

Pyšek P, et al. 2015. Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. Ecology. doi:10.1890/14-1005.1

Pyšek P, et al. 2018. Small genome separates native and invasive populations in an ecologically important cosmopolitan grass. Ecology 99: 79–90.

Pyšek P, et al. 2020. Scientists' warning on invasive alien species. Biological Reviews 95: 1511–1534.

Pyšek P, Richardson DM. 2007. Traits associated with invasiveness in alien plants: Where do we stand? Pages 97–125 in Nentwig W, ed. Biological Invasions. Springer.

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E. 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology and Evolution 23: 237–244.

Ravindra K, Rattan P, Mor S, Aggarwal AN. 2019. Generalized additive models: Building evidence of air pollution, climate change and human health. Environment International 132: 104987.

Rezende EL, Castañeda LE, Santos M. 2014. Tolerance landscapes in thermal ecology. Functional Ecology 28: 799–809.

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83: 263–282.

Ricciardi A, et al. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. Environmental Reviews 29: 119–141.

Ricklefs R, Wikelski M. 2002. Biodiversity reflects in part the diversification of life histories. Trends in Ecology and Evolution 17: 462–468.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022

Roman J. 2006. Diluting the founder effect: Cryptic invasions expand a marine invader's range. Proceedings of the Royal Society B 273: 2453–2459.
Rotter MC, Holeski LM. 2018. A meta-analysis of the evolution of increased competitive ability hypothesis: Genetic-based trait variation and herbivory resistance trade-offs. Biological Invasions 20: 2647–2660.
Ruland F, Jeschke JM. 2020. How biological invasions affect animal behaviour: A global, cross-taxonomic analysis. Journal of Animal Ecology 89: 2531–2541.
Sarà G, Romano C, Widdows J, Staff FJ. 2008. Effect of salinity and temperature on feeding physiology and scope for growth of an invasive species (*Brachidontespharaonis*, Mollusca: Bivalvia) within the Mediterranean Sea. Journal of Experimental Marine Biology and Ecology 363: 130–136.
Sardain A, Sardain E, Leung B. 2019. Global forecasts of shipping traffic and biological invasions to 2050. Nature Sustainability 2: 274–282.
Sax D, Stachowicz J, Gaines S. 2005. Species Invasions: Insights into Ecology, Evolution, and Biogeography. Sinauer Associates.
Schulz AN, Lucardi RD, Marsico TD. 2019. Successful invasions and failed biocontrol: The role of antagonistic species interactions. BioScience 69: 711–724.
Seebens H, et al. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences 115: E2264–E2273.
Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40: 415–436.
Shine R, Brown GP, Phillips BL. 2011. An evolutionary process that assembles phenotypes through space rather than through time. Proceedings of the National Academy of Sciences 108: 5708–5711.
Siefkes MJ. 2017. Use of physiological knowledge to control the invasive sea lamprey (*Petromyzonmarinus*) in the Laurentian Great Lakes. Conservation Physiology 5: cox031.
Sinclair BJ, et al. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecology Letters 19: 1372–1385.
Sinclair JS, Brown JA, Lockwood JL. 2020. Reciprocal human-natural system feedback loops within the invasion process. NeoBiota 62: 489–508.
Sinervo B, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899.
Skultety D, Matthews JW. 2017. Urbanization and roads drive non-native plant invasion in the Chicago metropolitan region. Biological Invasions 19: 2553–2566.
Sobek S, Rajamohan A, Dillon D, Cumming RC, Sinclair BJ. 2011. High temperature tolerance and thermal plasticity in emerald ash borer *Agrilusplanipennis*. Agricultural and Forest Entomology 13: 333–340.
Soeharjono S, Roche DG. 2021. Reported individual costs and benefits of sharing open data among Canadian academic faculty in ecology and evolution. BioScience 71: 750–756.
Sotka EE, et al. 2018. Combining niche shift and population genetic analyses predicts rapid phenotypic evolution during invasion. Evolutionary Applications 11: 781–793.
Steury TD, Murray DL. 2005. Regression versus ANOVA. Frontiers in Ecology and the Environment 3: 356–357.
Steury TD, Wirsing AJ, Murray DL. 2002. Using multiple treatment levels as a means of improving inference in wildlife research. Journal of Wildlife Management 66: 292–299.
Suda J, Meyerson LA, Leitch IJ, Pyšek P. 2015. The hidden side of plant invasions: The role of genome size. New Phytologist 205: 994–1007.
Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. 2014. Abiotic and biotic stress combinations. New Phytologist 203: 32–43.
Symonds MRE, Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65: 13–21.
Tepolt CK. 2015. Adaptation in marine invasion: A genetic perspective. Biological Invasions 17: 887–903.
Tepolt CK, Somero GN. 2014. Master of all trades: Thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinusmaenas*. Journal of Experimental Biology 217: 1129–1138.
Terblanche JS, Hoffmann AA, Mitchell KA, Rako L, le Roux PC, Chown SL. 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. Journal of Experimental Biology 214: 3713–3725.
Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11: 2234–2250.
Tiatragul S, Hall JM, Warner DA. 2020. Nestled in the city heat: Urban nesting behavior enhances embryo development of an invasive lizard. Journal of Urban Ecology 6: 1–11.
Tremblay N, Guerra-Castro EJ, Díaz F, Rodríguez-Fuentes G, Simões N, Robertson DR, Rosas C. 2020. Cold temperature tolerance of the alien Indo-Pacific damselfish *Neopomacentruscyanomos* from the southern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology 524: 151308.
Uden DR, Allen CR, Angeler DG, Corral L, Fricke KA. 2015. Adaptive invasive species distribution models: A framework for modeling incipient invasions. Biological Invasions 17: 2831–2850.
Van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235–245.
Verberk WCEP, Overgaard J, Ern R, Bayley M, Wang T, Boardman L, Terblanche JS. 2016. Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. Comparative Biochemistry and Physiology A 192: 64–78.
White EM, Wilson JC, Clarke AR. 2006. Biotic indirect effects: A neglected concept in invasion biology. Diversity and Distributions 12: 443–455.
Whitney KD, Gabler CA. 2008. Rapid evolution in introduced species, "invasive traits" and recipient communities: Challenges for predicting invasive potential. Diversity and Distributions 14: 569–580.
Williams JL, BE Kendall, Levine JM. 2016. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. Science 353: 482–485.
Willson JD. 2017. Indirect effects of invasive Burmese pythons on ecosystems in southern Florida. Journal of Applied Ecology 54: 1251–1258.
Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM. 2009. Something in the way you move: Dispersal pathways affect invasion success. Trends in Ecology and Evolution 24: 136–144.
Wingfield JC, Krause JS, Perez JH, Chmura HE, Németh Z, Word KR, Calisi RM, Meddle SL. 2015. A mechanistic approach to understanding range shifts in a changing world: What makes a pioneer? General and Comparative Endocrinology 222: 44–53.
Wonham MJ, Walton WC, Ruiz GM, Frese AM, Galil BS. 2001. Going to the source: Role of the invasion pathway in determining potential invaders. Marine Ecology Progress Series 215: 1–12.
Zettlemoyer MA, Schultheis EH, Lau JA. 2019. Phenology in a warming world: Differences between native and non-native plant species. Ecology Letters 22: 1253–1263.
Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer.

Leigh Boardman (leigh.boardman@memphis.edu) is affiliated with the Department of Biological Sciences and with the Center for Biodiversity Research at the University of Memphis, in Memphis, Tennessee, in the United States. Julie Lockwood is affiliated with the Department of Ecology, Evolution, and Natural Resources at Rutgers University, in New Brunswick, New Jersey, in the United States. Mike Angilletta is affiliated with the School of Life Sciences and with the Center for Learning Innovation in Science at Arizona State University, in Tempe, Arizona, in the United States. Jesse Krause is affiliated with the Department of Biology at the University of Nevada, in Reno, Nevada, in the United States. Jennifer A Lau is affiliated with the Department of Biology at Indiana University, in Bloomington, Indian, in the United States. Michael Loik is affiliated with the Environmental Studies Department at the University of California, Santa Cruz, in Santa Cruz, California, in the United States. Daniel Simberloff is a fossil entombed in the Department of Ecology and Evolutionary Biology at the University of Tennessee, in Knoxville, Tennessee, in the United States. Christopher J. Thawley is affiliated with the Department of Biological Sciences at the University of Rhode Island, in Kingston, Rhode Island, in the United States. Laura A. Meyerson is affiliated with the Department of Natural Resources Science at the University of Rhode Island, in Kingston, Rhode Island, in the United States.

Downloaded from https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biac080/6709233 by CDL - California Digital Library user on 05 October 2022