Trends in Ecology & Evolution

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Opinion

Community Physiological Ecology

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The effects of animal homeostatic function on ecological interactions have not been well-integrated into community ecology. Animals mediate environmental change and stressors through homeostatic shifts in physiology and behavior, which likely shape ecological interactions and plant communities. Animal responses to stressors can alter their habitat use, selective foraging, and stoichiometry, which can in turn affect trophic interactions, plant growth, reproduction, and dispersal. Here, we describe a community physiological ecology framework that integrates classical ecological theory and emerging empirical approaches to test how animal homeostatic responses to environmental change mediate ecological interactions and shape communities. Interdisciplinary approaches could provide essential data to characterize and forecast community responses to rapid global environmental change.

Highlights

Homeostatic control via physiology mediates habitat use, foraging behavior, prey selection, and even risk-taking behaviors in all animals.

Changes in physiology or behavior of individual animals likely cause ecological cascades detectable in the structure of communities and ecosystem processes.

Our capacity to link individual physiology and behavior to community dynamics has often been hampered by technological limitations.

Rapidly emerging methods and technologies (e.g., pharmacological implants that manipulate homeostatic control in free-ranging animals, high-resolution tracking technology, and stable isotope tracers capable of tracking plant materials through food webs) make new integrative studies possible that link individual processes to large scale ecological dynamics in a changing world.

Emerging Approaches for Testing Large Scale Ecological Interactions at the Individual Level

A primary question in ecology is how dynamic interactions among abiotic factors, consumers, and producers shape ecosystems [1–3]. In exploring this question, decades of ecological research have provided substantial evidence demonstrating that both bottom-up (e.g., abiotic conditions) and top-down (e.g., animal foraging behavior) factors influence plant communities and biodiversity patterns (Figure 1). Concurrent research by physiological ecologists has demonstrated that animal physiology plays a critical role in determining how animals interact with their environment [4–7]. Explicitly integrating these two disciplines, which have often been separate, through the use of emerging technology to examine how consumer physiology mediates ecological interactions could reveal overlooked drivers of community and ecosystem ecology.

Here, we argue that underappreciation of physiology in community ecology has limited our mechanistic understanding of the roles animals play in shaping many ecological dynamics including predator–prey interactions, foraging and food selection [8,9], pollination [5], and plant growth and nutrient cycling [10,11] (Figure 1). The concept that physiological processes at the individual animal level can affect entire ecosystems has been suggested previously [6,7,12–14]. In order to explicitly integrate and build upon this research, we propose a framework for community physiological ecology. This framework hypothesizes that the physiological state of an animal alters its behavior, which can affect species interactions and alter community structure and function (Figure 2). The physiological state of an animal includes diverse homeostatic processes, including endocrine stress function, thermoregulation, osmoregulation, immune function, and nutrient stoichiometry. Furthermore, we suggest that we can now leverage emerging technologies to conduct novel experimental tests across biological scales (Figure 1).

Linking Consumer Homeostatic Physiology to Ecological Community Dynamics

Animals maintain homeostasis through physiological responses to environmental factors that in turn mediate interactions between the environment and animal behavior. For example,

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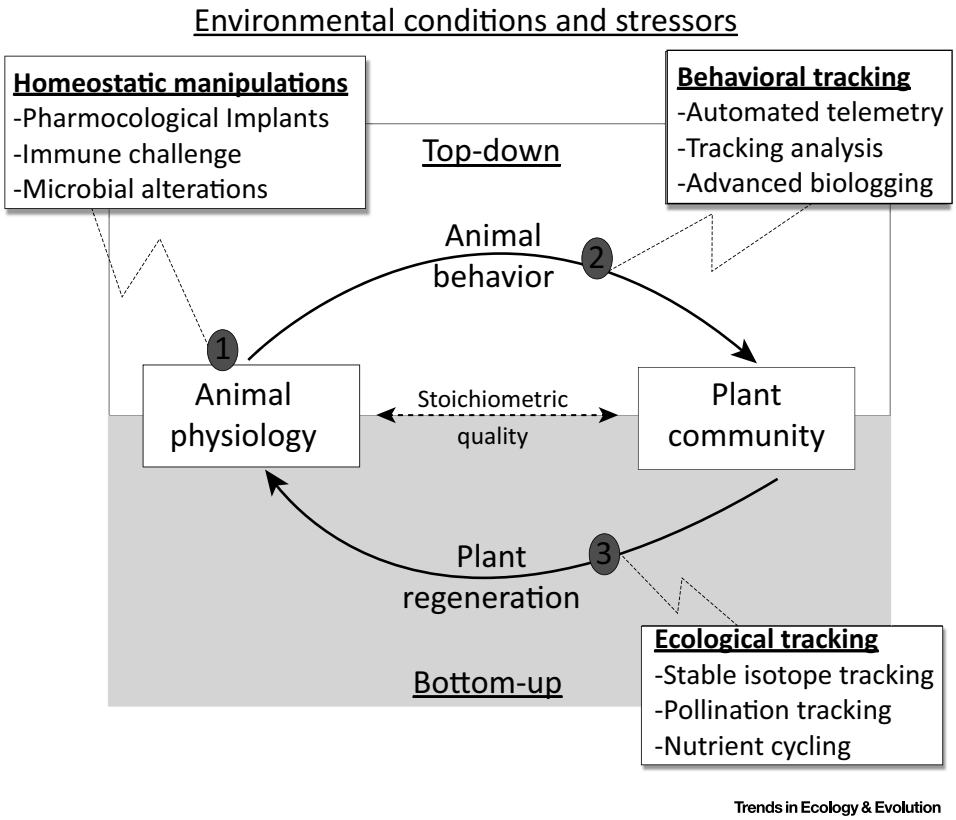

Figure 1. Physiological and Behavioral Dynamics in Animals (Nodes 1 and 2) Constitute Homeostatic Mechanisms by Which Animals Balance Life-Sustaining Requirements with Responses to Environmental Variation and Potential Stressors (surrounding box). Emerging technologies (broken bolts) provide novel approaches to manipulate and track how interactions between consumer physiology and behavior and plant dynamics (Node 3) mediate the classic top-down and bottom-up processes that shape ecological communities in a changing environment.

neuroendocrine regulatory axes and secretory hormones are central mechanisms by which vertebrates and invertebrates alike regulate diverse homeostatic processes while coping with environmental challenges, including anthropogenic disturbances [15,16]. Stress hormones are among the most-well-explored homeostatic regulators of ecological interactions. Elevated stress hormones mobilize energy and nutrient stores, and increase metabolism to fuel fight or flight responses to both short- and long-term stressful conditions. Presumably, increased metabolism and nutrient demand translate into behavioral changes in habitat use, foraging patterns, food selection, and nutrient stoichiometry of excreta and body tissues [4,6,8,17–19]. Such physiological and behavioral responses could alter ecological interactions and plant communities through selective foraging, changes in predator–prey dynamics, nutrient cycling, and other trophic and community interactions [3,6,11]. The ecological effects of other homeostatic processes such as thermoregulation, osmoregulation, and immunity have generally not been tested, but should similarly affect community dynamics [3,20–22] (Table 1).

Determining the effects of animal physiological functioning on broader ecological processes is an underexplored research direction with potential for rapid growth in the next decade, much like the emerging field of conservation physiology has expanded our capacity to test and understand how organisms respond to changing environments [23]. While there are definite

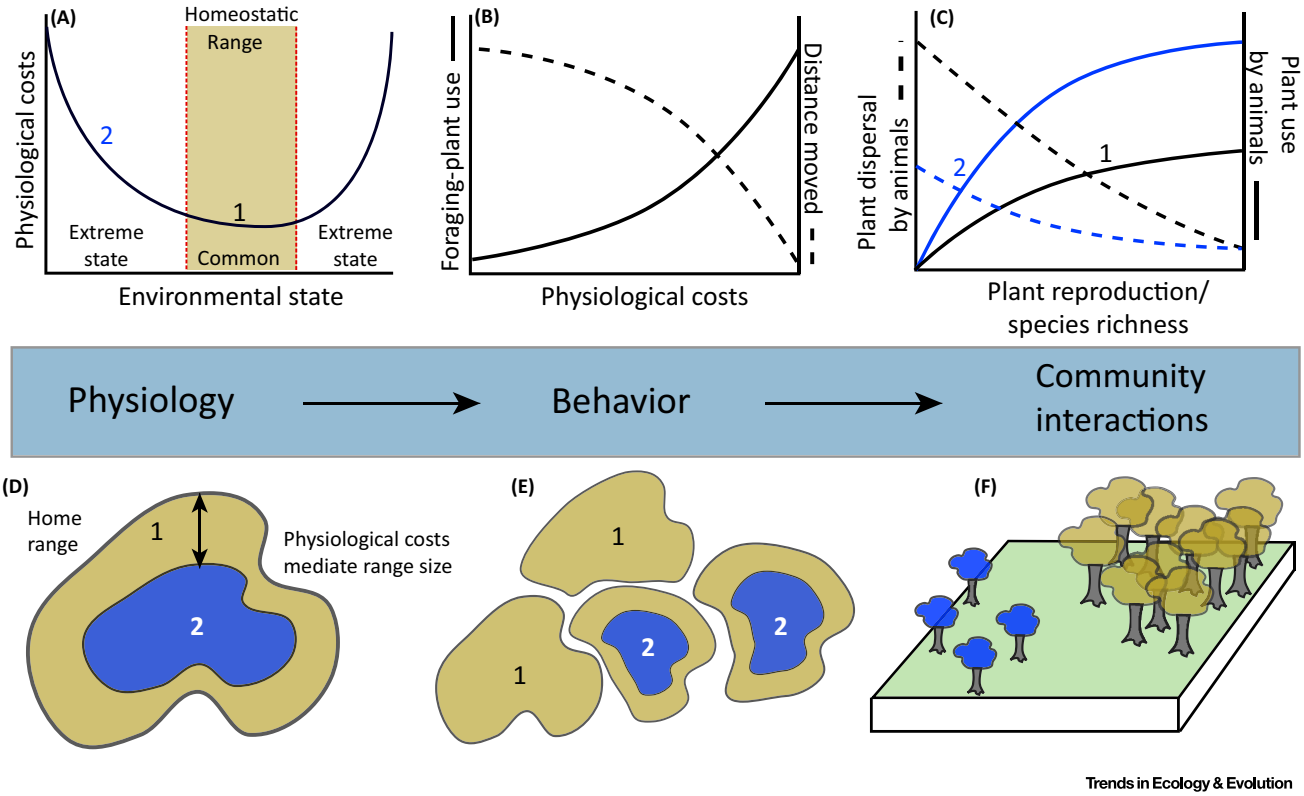

Figure 2. Community Physiological Ecology Integrates the Physiological Costs of Maintaining Homeostasis for Animals in variable Environmental States That May Include Extremes Imposed by Anthropogenic Change (A). Physiological, homeostatic responses to change often incur costs (i.e., energy and nutrients) and induce animals to alter behavior aimed at balancing costs (e.g., increased foraging or selectivity) (B, D). Altered behavior, mediated by physiology, likely influences ecological interactions (e.g., territoriality, pollination, or seed dispersal) (E). These interactions suggest a predictive framework for developing and testing hypotheses for how plant communities may be affected (C, F). Given a stable environment, plant reproduction and community species richness as mediated by animals settle at an equilibrium, (C, State 1, black lines), where animal ecological interactions are a balance of plant-negative (e.g., herbivory) and plant-positive effects (e.g., seed dispersal). However, as environmental conditions impose homeostatic costs on animals, this framework predicts shifts in plant reproductive success and community richness that will shift to new equilibrium states as mediated by consumer behavior (C, State 2, blue lines). This framework describes a mechanism by which plant community form and function might change with imposition of environmental stressors that do not directly affect the plants themselves (Figure 2D–F).

needs for descriptive work on patterns in physiological parameters across biological scales from individuals through populations and communities, we believe the real leaps in our mechanistic understanding of community and ecological function will be gained through experimental manipulations of animal homeostasis and tracking of subsequent ecological interactions at varied scales ranging from local communities to landscapes (Figure 2).

Community Physiological Ecology

Community physiological ecology integrates ideas from classical ecological theory (e.g., optimal foraging theory and island biogeography theory) and emerging empirical approaches to develop testable hypotheses regarding how physiological costs of maintaining homeostasis for animals influence communities and ecosystems (Figure 2). Generally, as environmental states shift outside a common range (denoted as State 1), animals must use physiological mechanisms (e.g., thermoregulation or osmoregulation) to counter these forces (denoted as State 2) and maintain homeostasis (Figure 2A). Such homeostatic responses incur energy, nutrient, and water costs. To meet these costs and correct imbalances, animals are predicted to alter

Table 1. Examples of Physiological Systems That May Be Appropriate for Manipulation in Order to Study the Effects of Animal Homeostatic Function on Community and Ecosystem Dynamics

Homeostatic factor	Possible anthropogenic stressors	Possible physiological mediators	Possible behavioral mediators	Possible ecological effects	Example study systems	Refs
Energy balance	Climate change	Neuroendocrine regulatory axes	Foraging	Plant growth and diversity	Stress hormones increase foraging/ingestion	[50,51]
	Habitat destruction	Stress hormones	Altered habitat use	Predation	Early life stress shapes foraging in adults, can influence phenotypes across generations	[52]
	Urbanization			Pollination and seed dispersal	Foraging success is related to stress hormone in seabirds	[53]
	Invasive species			Stoichiometric changes to animals and nutrient cycling	Stress affects spatial learning in pollinating bees	[5]
Water balance	Drought	Hypothalamus-posterior Pituitary–kidneys	Water intake	Predator–prey relationships	Relative humidity, water/nectar concentrations influence moth foraging and pollination	[24]
	Altered water/nectar sources	Vasopressin hormone	Nitrogen/water excretion	Pollination rates, dispersal distance	Water balance effects trophic interactions	[21]
	Engineering of water resources	Diuretic peptides	Lipid intake (metabolic water)	Plant growth and diversity	Water balance shapes rodent foraging	[25]
			Selective foraging			
Nutrient balance	Elevated stress hormones	Neuroendocrine–vagus nerve	Selective Foraging	Nutrient cycling	Many taxa alter foraging in response to stress	[8]
	Altered nutrient availability	Microbiome		Plant growth and diversity	Insects vary diet selection and foraging in response to micronutrient needs	[54]
	Pollution	Gastrointestinal function				
	Monoculture agricultural practices					
Thermoregulation	Climate change	Hypothalamus–pituitary	Water use	Trophic effects	Ungulates alter foraging behavior and habitat use in response to heat stress	[26]
	Urban heat islands	Cardiovascular	Habitat use	Pollination	Ectotherms increase selective foraging with increased temperatures	[55,56]
		Evaporative cooling	Refuge use		Small mammalian herbivores alter selective foraging and consumption with temperature	[22]
		Enzyme and muscle performance	Diurnal patterns		Bees forage less when heat stressed	[57]
Ecoimmunological function	Invasive parasites	Innate immune system	Selective foraging	Pollination	Foraging behavior and costs altered by infection	[58,59]
	Emerging disease	Adaptive immune system	Self medication	Plant growth	Animals self-medicate through selective foraging of plants	[60]
	Pollution			Plant community diversity		

behavior by increasing intake (e.g., through increased foraging efforts or shifts in food selection), or decreasing expenditures (e.g., by limiting movements) (Figure 2 B,D). These behavioral changes will then shift the relative balance of plant-negative (e.g., seed consumption) and plant-positive interactions (e.g., seed dispersal) with the physiological state of the animal (Figure 2C). This model suggests requirements for plant reproductive success (e.g., pollination, seed set, and germination) and subsequent community diversity can be mediated by animal use of plants (e.g., herbivory, seed consumption vs. caching) and animal dispersal of plant propagules (Figure 2C). To over-simplify, imagine under common environmental states, plant diversity stabilizes at some equilibrium (Figure 2C, State 1, black lines). As environmental conditions impose homeostatic costs on animals, the framework predicts shifts to new equilibrium states in plant reproductive success and community richness (Figure 2C, State 2, blue lines). At the community or landscape scale, the footprint of stressed consumers could shrink (Figure 2E) and thereby alter plant distribution and community structure (Figure 2F). Homeostatic disruption in an animal species could also extend across trophic levels to alter predator–prey interactions and competition among consumers, thereby indirectly altering plant dynamics. This framework thus describes an experimental approach to disentangle the direct and indirect effects of environmental stressors on animals, plants, and trophic interactions across food webs (Figure 2D–F).

As a hypothetical example, consider a simple plant–pollinator community in a region that experiences periodic drought. The plant community might change in direct response to drought, and/or indirect effects of osmoregulatory function in pollinators. To disentangle these two pathways, one could pharmacologically manipulate osmoregulatory function of the pollinators during nondrought years. Movement behavior of the animals could be subsequently tracked with digital telemetry to test if landscape-level foraging patterns are changed or if nectar consumption increases to meet water demand (Figure 2B). Indeed, insect foraging and pollination shift with drought states, whereby insects target sources with higher water or nectar availability [21,24]. This hypothetical situation extends to other consumers. For example, granivorous rodents shift foraging, seed predation, and caching patterns in relation to water balance [25], and large herbivores shift habitat use and forage patterns in response to temperature and water stress [26]. Similarly, water or nutritionally stressed predators can select prey to prioritize high water content or specific nutrients to balance homeostatic needs [27,28]. So the framework could also be applied to predators to test for effects of homeostatic costs on trophic cascades and food web dynamics. Isotopic tracers, dyes, or DNA metabarcoding would then allow for tracking of changes to distribution patterns of pollination, granivory, seed dispersal, predation, and herbivory within animal home ranges or experimental plots [29–31]. Although it might not be logistically practical in all cases, plant growth, reproduction, and even gene flow could be followed among plots for months, seasons, or years. Community physiological ecology provides a means to make explicit predictions about each step of this process. In these cases, we might predict that osmoregulatory stress will lead to more localized movements by the consumers to limit locomotion costs and conserve water (Figure 2A,B), which will have cascading effects on plant pollination/dispersal, vegetative growth, species distribution, and plant community diversity (Figure 2B,C).

Manipulation of Animal Homeostatic Physiology

Documenting cascading animal physiological effects from individuals to ecosystems has been hampered by our ability to manipulate animals in the field and track their impacts on ecological interactions and ecosystem functioning, but emerging technologies are opening exciting new avenues of inquiry (Table 1). First, techniques to assess and experimentally manipulate animal physiological states are becoming more common and widely applicable.

Subdermal implants allow for extended release of pharmacological compounds that can alter specific physiological processes, such as circulating glucocorticoid stress hormones that can be elevated or suppressed to mimic exposure to environmental stressors [32]. Osmoregulatory responses to dehydration can be manipulated by implants containing diuretic compounds such as furosemide and hydrochlorothiazide [33]. Perceived disease states and immune responses can be manipulated by endotoxin (e.g., lipopolysaccharide and peptidoglycan) injections or implants that induce febrile responses and acute sickness behaviors in animals (Figure 2A,B) [34]. Energetic pathways, thermoregulatory responses, and feeding behavior can be manipulated with, for example, 2-deoxy-d-glucose, ketones, or mercaptoacetate [35]. Coupling physiological manipulations with analysis of relevant homeostatic responses to varied environmental conditions (e.g., hormone enzyme immunoassay, water balance, and thermoregulation) can provide context and validation that experiments are ecologically relevant and confirm that manipulations do not harm animals or their welfare [36–38]. The next step is to link homeostatic manipulations to behavioral and ecological interactions.

Emerging Technologies for Biologging and Automated Tracking of Animal Behavior

Emerging technology in automated biologging and tracking of animal movement can link homeostatic behavioral changes to shifts in community interactions (Figure 2). Advances in biologging, including automated digital telemetry with wireless networking, global positioning system (GPS) miniaturization, accelerometers, and physiological loggers, are expanding possibilities for detailed tracking of diverse animals [39–41]. Automated telemetry systems now use lightweight and long-lasting transmitters incorporating cellphone GPS technology, some of which are solar powered and miniaturized for tagging of even small animals [40,42]. Additionally, coupling biologgers such as accelerometers with GPS can provide detailed contextual information to link animal homeostatic function with ecological interactions, and can even be used to infer internal states such as stress or disease conditions [41,43,44]. For example, through integrating several biologgers one can imagine demonstrating how nutritional stress (or disease) in large herbivores shifts habitat use and diet selection to balance dietary needs (or immunity) [26]. Furthermore, analysis of tissues or feces for hormones, nutrient condition, or DNA barcoding could link animal states to changes in behavior and plant consumption (Figure 2B,C).

Linking Consumers to Plant Regeneration, Reproduction, and Dispersal

The final piece of the community physiological ecology framework closes the loop between bottom-up and top-down forces by linking animal physiology and behavior to plant fitness, community dynamics, and ecosystem processes such as nutrient cycling (Figure 2C). Stable isotopes, dyes, seed telemetry, and DNA metabarcoding approaches can provide powerful tools [30,31,45–47] to link physiologically mediated shifts in consumer behavior to plant regeneration, growth, and reproduction. For example, application of isotopically labeled solutions to foliage results in highly enriched vegetation, seeds, and even seedlings that can be used to track pollination, herbivory, granivory, and germination patterns across a landscape [45]. While recovering labeled plant components from the environment (e.g., seeds) can be challenging, clever application in plots distributed within animal home ranges (determined by telemetry) coupled with sampling of animal tissues (e.g., blood or feces), and environmental samples collected relative to labeled plots [29] could effectively link animal homeostatic states and foraging to plant community dynamics (Figure 2D–F).

Concluding Remarks and Future Perspectives

Changing environmental conditions can impose stress to diverse and interacting animal homeostatic systems, each of which provide distinct opportunities to test how disturbance to the environment and anthropogenic global change may impact animals and the communities they inhabit (Table 1). Integrating manipulation of homeostatic systems with biologgers and tracking of how animals use environmental resources (e.g., isotopes or dyes) can detail how animal responses to changing environmental factors can impact ecological interactions. Animal water balance, for example, is a promising avenue for future inquiry that has largely been overlooked as a potentially important factor shaping top-down interactions in terrestrial food webs [21,25,48]. The effects of shifts in animal homeostatic function could also extend across multiple trophic levels, whereby water stressed predators, for example, could alter foraging patterns to prioritize water balance rather than energy or nutrients, thereby altering community dynamics [27,28]. Attaching biologgers to manipulated and unmanipulated animals across trophic levels, including predators, prey, and competitors within grids monitored by automated telemetry systems could provide compelling tests of whether shifts in animal homeostasis have cascading effects across food webs and communities [3]. Finally, shifts in homeostatic function in response to stressors could impart legacy effects through generations of animals that affect future community dynamics. Accumulating evidence suggests that exposure to stressors can cause lasting alterations to the phenotypes of organisms and their offspring via epigenetics (e.g., chromatin modifications or DNA methylation). Epigenetic changes in animals can affect ecologically important traits in relation to environmental conditions including foraging behavior, responses to interspecific interactions, and disease susceptibility, which as detailed above could have long-term consequences for community structure and function (see Outstanding Questions) [49].

Experimental manipulation of specific homeostatic systems will enable ecologists to reveal how animal physiology and behavior mediate or modify effects of increased temperature, drought, parasite emergence, or invasive species on ecological communities and ecosystems. To date, integration of animal homeostatic function into community ecology has been rare, but studies in this emerging field (Table 1) suggest such interdisciplinary approaches may provide novel and even essential data to characterize and forecast community responses to environmental change. Initially, the ease with which these approaches can be comprehensively tested will likely vary across ecosystems. Ecosystems that are more spatially or temporally discrete (e.g., deserts with pulsed precipitation and flowering) or communities that are more contained (e.g., pollinator or seed disperser networks) could be more amenable for initial tests of the community physiological ecology framework. Ultimately, however, innovative manipulation of animal physiology in diverse natural systems in conjunction with advanced biologging and tracking technologies of animal and plant responses will allow for explicit tests of how consumer homeostatic function contributes to community and ecosystem dynamics in a changing world.

Outstanding Questions

How does the water balance of animals shape foraging behavior, diet selection, trophic interactions, and ecological communities?

How do homeostatic shifts in animal physiology and behavior influence interactions across multiple trophic levels?

What are the effects of immune responses to acute and chronic infections in animals on trophic interactions?

Are there legacy effects of shifts in homeostatic function across generations of animals on ecological communities via epigenetics?

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