Trends in
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Opinion

Extended phenotypes: buffers or amplifiers of climate change?

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Historic approaches to understanding biological responses to climate change have viewed climate as something external that happens to organisms. Organisms, however, at least partially influence their own climate experience by moving within local mosaics of microclimates. Such behaviors are increasingly being incorporated into models of species distributions and climate sensitivity. Less attention has focused on how organisms alter microclimates via extended phenotypes: phenotypes that extend beyond the organismal surface, including structures that are induced or built. We argue that predicting the consequences of climate change for organismal performance and fitness will depend on understanding the expression and consequences of extended phenotypes, the microclimatic niches they generate, and the power of plasticity and evolution to shape those niches.

Highlights

All organisms modify their local conditions by exchanging materials and energy with their environments. Many organisms also induce or build external structures around themselves, which are considered extended phenotypes.

External structures play central roles in determining the microclimates that organisms experience. Depending on their materials, architecture, and location, they may buffer or amplify local climate variability and macroclimatic change. To date, however, no general frameworks are available for predicting the microclimatic effects of these structures.

The importance of extended phenotypes during climate change will depend on whether they exhibit adaptive plasticity and how rapidly they evolve in response to climate variability.

Extended phenotypes and organismal responses to climate change

Among biologists, a rough consensus has emerged about the biological effects of climate change [1]. The consensus in part reflects widespread agreement about how climates around the globe are changing [2]. It also reflects a shared view of causality in which organisms react physiologically and behaviorally to externally imposed shifts in climate. This philosophy is exemplified by the use of **species distribution models** (see Glossary) and environmental niche models to forecast climate-related vulnerability [3,4], and by **mechanistic models** that explicitly consider organismal performance in relation to variable abiotic conditions (primarily temperature) and organismal tolerance limits [5]. Such models have been extended recently by agent-based models [6] that explicitly include behavioral plasticity [7] and by integral projection models that integrate information on genetics, population structure, individual states, stochasticity, and climate to predict evolutionary trajectories [8].

Here, we propose that the predictive utility of these models may be enhanced by considering an underappreciated component of climate–organism interactions: that organisms alter their experience of climate via their **extended phenotypes**. Extended phenotypes refer to traits that extend beyond an organism's surface into the environment surrounding it, as articulated from the point of view of genes by Dawkins [9] and of organisms by Turner [10].

Extended phenotypes are remarkably common [11] (Figure 1). They include externally induced or **built structures** such as burrows and nests of mammals and birds, the nests of termites and ants, organisms which account for a large fraction of animal biomass on earth, and the many structures induced or constructed by arthropods in different phases of their life cycle, including galls, feeding galleries, burrows, above-ground nests, pupation structures, and reproductive structures. Extended phenotypes also emerge when organisms exchange energy and materials with their local environments [12] or modify the structure or texture of local materials [10,13]. Importantly, many species use structures built by other species, with varying levels of maintenance or modification of the structure required and, in some instances, substantial energetic consequences (e.g., [14]); the link between extended phenotype and **ecosystem engineering** is tight.

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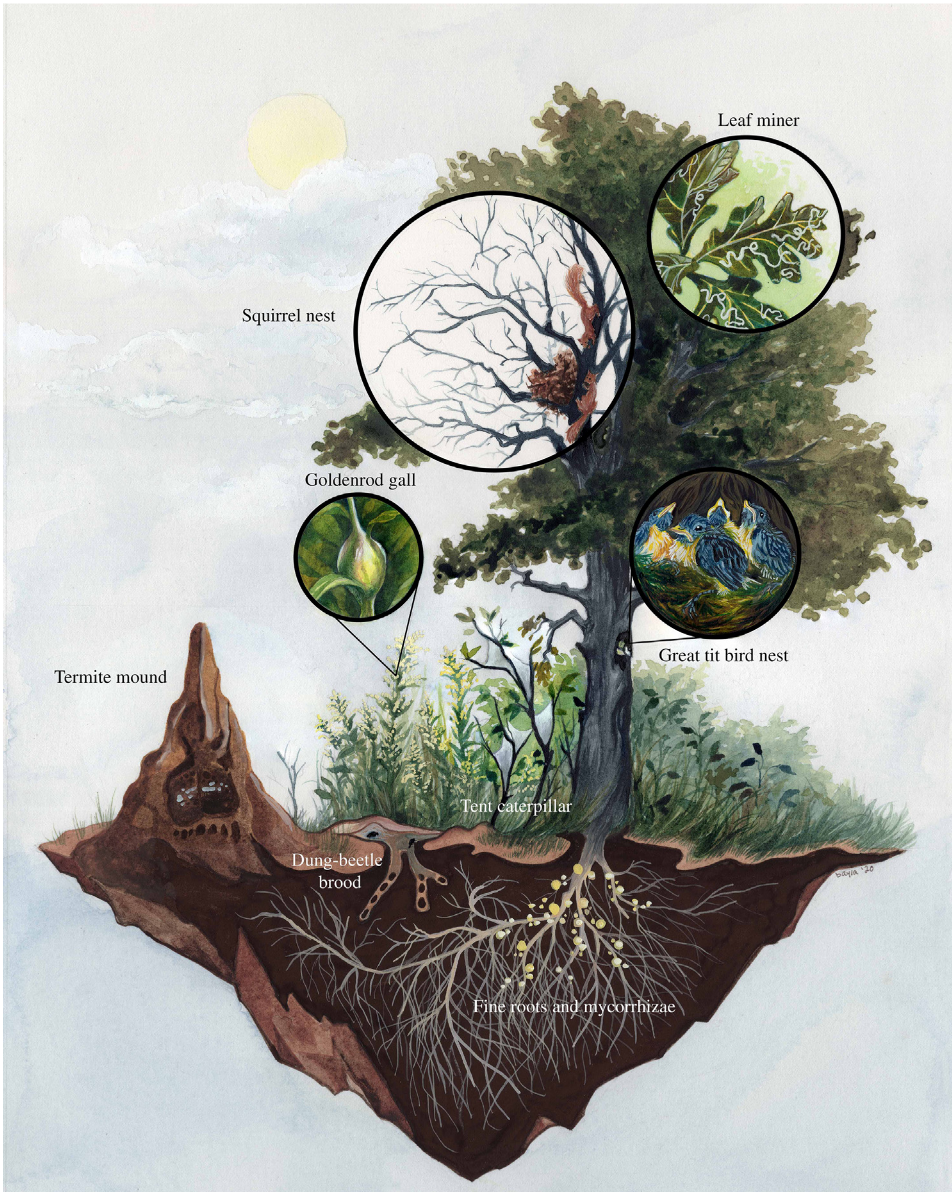


Trends in Ecology & Evolution

Figure 1. Examples of extended phenotypes and the microclimatic niches that they produce. Extended phenotypes determine how organisms experience climate (painting by Bayla Arietta). Larvae of many insects create leaf mines as they consume internal leaf tissues. Mines provide high humidities and are warmer than ambient air when the mine is illuminated with sunlight (buffer in cold conditions, amplify in warm) [68,69]. In winter, nests of the squirrel *Sciurus vulgaris* provide enough insulation that **metabolic heat** can raise nest temperatures 20–30°C above ambient air temperatures (buffer [70]). Goldenrod (*Solidago*) galls are induced by larvae of the fly *Eurosta solidaginis*. Direct sunlight can raise gall temperatures substantially over air temperature (amplifier [71]). Mounds of the African termite, *Macrotermes michaelseni*, harness solar and metabolic heat and ambient wind to drive internal gas flows, stabilizing internal gas levels and temperatures (buffer [72,73]). Larvae of dung beetles in the genus *Onthophagus* feed, grow, and develop within underground balls of dung constructed by their mothers, benefitting from dampened temperature fluctuations [74] and from structural and microbial/nutritional modifications to their dung balls (buffer [75]). In direct sunlight, communal silk tents built by caterpillars can reach temperatures far above ambient air temperature (buffer in cold climates, amplifier in warm). Temperature mosaics across sunny and shady sides are also used for **behavioral thermoregulation** (buffer [76]). Forest canopies stabilize temperatures below the canopy and into the ground, which supports growth of fine roots and mycorrhizae (buffer, Box 1). Great tits construct heavier, more insulated nests when the weather is colder in the week before clutch initiation (buffer [77]).

Glossary

Behavioral thermoregulation: achieving desired body temperature by moving throughout locally available mosaics of operative temperature.

Bogert effect: behavioral flexibility allows organisms to avoid extremes and therefore dampen selection on morphological and physiological traits. Such an effect can slow rates of morphological and physiological evolution.

Built structures: (e.g., nest/tent/shelter/burrow); animal-built structures or spaces used by animals to seek refuge for some part of their life cycle, or to overwinter, that may be considered as forms of extended phenotypes.

Ecosystem engineering: often derived from extended phenotypes and is similar to niche construction, but with more pervasive effects on whole communities in space and time.

Extended phenotype: phenotypes of organisms that extend beyond their integuments into the environment.

Heat budget: an accounting of gains and losses of heat through different pathways [often measured in joules per second (Watts), sometimes per unit surface area], including conduction, convection, radiation, metabolism, and evaporation/condensation. When an ectotherm achieves a steady-state (stable) temperature, gains and losses of heat are balanced.

Mechanistic model: a biological process-based model in which organismal traits are used to infer population dynamics, geographic distribution, or environmental constraints. While these models have become increasingly sophisticated and computationally intensive, covering diverse aspects of organism–environment relationships, to our knowledge none/few studies have explicitly examined the impact of variation in the extended phenotype on organismal traits and fitness in a climate change context.

Metabolic heat: heat produced by the sum of all of chemical reactions occurring inside a living organism. Heat output occurs because chemical transformations are inefficient and rate of heat output can be used as a measure of metabolic rate.

Microclimate: climatic conditions at small spatial scales surrounding individual organisms or colonies.

Depending on size, materials, and structure, extended phenotypes may buffer or amplify the effects of climate change and any such effects may be age- or time-dependent. The consequences of extended phenotypes for the organisms that build them will depend critically on the kinds and magnitudes of plasticity that extended phenotypes exhibit, on heritabilities of underlying behavioral and physiological traits, and on how plasticity shapes selection on the entire organism–extended phenotype system. Because temperature in terrestrial systems is the focus of most published studies, our ideas in the following text reflect this bias. Nevertheless, climate change is multifactorial (i.e., involving diverse concurrent stressors) [2] and the general ideas apply also to other physical factors and to marine and freshwater biomes.

The origin of microclimatic niches

Individuals live in localized sets of conditions, their **microclimates**, which have extents that scale to body size [15]. It is well known that organisms can modify their microclimatic experience by moving among local patches [7,16,17]. Moving even a few millimeters or centimeters, for example, may be enough to alter body temperatures by 5–10°C for small leaf-dwelling arthropods [18], for intertidal gastropods [19], or for spiders exploiting vertical temperature gradients under rocks into the soil [20]. The spatial configuration of such local mosaics, and the capacity of organisms to move within them, can be critically important for avoiding thermal stress [18,21,22] and thus for coping with more frequent high-temperature events during climate warming [23].

Both movement and extended phenotypes are forms of **niche construction**, which refers broadly to the effects that organisms have on their local habitats and microclimates [24–26]. A key idea in niche construction is that altered conditions constructed in part by the organisms themselves feedback to affect their own performance, ecology, and evolution. In this sense, extended phenotypes and niche construction are complementary: calling an external structure or condition ‘an extended phenotype’ emphasizes the role of the organism in building or shaping it, whereas calling it ‘niche construction’ emphasizes its feedback onto the performance and fitness of the organism [12].

The microclimatic niches produced by extended phenotypes determine how individuals experience climate variation and climate change (Figure 1 and Box 1). In particular, they determine how much warming is transferred into the extended phenotype (the structure) and to what extent plasticity in structure, use of materials, or design can alter organismal performance via changes in the construction of the microclimate. Indeed, shifts in climate that switch a buffering structure into an amplifying structure, with effects that cannot be combatted via plasticity, may trap organisms and populations in destructive microclimatic extremes of their own making. Conversely, effective buffering via plasticity can minimize the negative effects of climate change. We expect also that the structure and function of extended phenotypes will vary with climatic gradients (e.g., latitude, altitude). For example, we predict that extended phenotypes from cold climates will generally function to warm microclimates above local ambient air temperatures or to prevent heat loss from organisms, whereas extended phenotypes from warm climates will exhibit cooling functions. These expectations appear to be fulfilled by intra- and interspecific variation in the morphology of bird nests, which show strong correlations with climatic conditions [27]. Zebra finches, for example, build larger, warmer nests in cool conditions [28], while the dome (a roof of grass built over the nest cup) may shade eggs and chicks and keep them from overheating in very hot conditions [29].

Extended phenotypes as amplifiers or buffers

An extended phenotype can alter environmental fluctuations depending on the dynamics of the **heat budget** [15], with outcomes reflecting two biophysical rules. First, size matters. In the same way that larger ectotherms have longer time constants for heating and cooling [30], so do larger structures that animals build. Larger constructed niches dampen thermal fluctuations,

Relevant conditions include air temperature and humidity, wind speed, surface temperature, and radiative environment, including both longwave radiation from the sun, sky, and nearby objects and shortwave radiation from the sun. Microclimatic conditions can differ strongly from nearby macroclimates and often show much higher spatial diversity and more rapid temporal fluctuations (e.g., in response to clouds passing in front of the sun).
Modularity: a system or network property that describes the degree to which different compartments can be decoupled into separate clusters. Trait modularity influences the degree to which interconnected sets of functional traits may evolve independently of one another. Because extended phenotypes often reflect behaviors of their builders, understanding the relative modularity of suites of behaviors will be important for predicting patterns of plasticity and evolution of extended phenotypes.
Niche construction: the process of organisms or colonies or communities altering their local microclimates by means of their activities or efforts to construct objects/artifacts.
Species distribution model: correlative approach to estimating expected distributions of organisms (usually assumed to approximate the fundamental niche) whereby point locations of organisms are associated with suites of environmental variables at those locations to infer suitable conditions for species persistence.

Box 1. The collective extended phenotype of forest trees creates a buffered thermal niche

We view extended phenotypes as a continuum of structures from simple to complex and involving little to great amounts of organismal time and resources. Extended phenotypes may also result in a continuum of microclimate effects that may not scale with organismal effort, or (vice versa) small changes in traits may lead to large microclimatic effects. Although some examples of extended phenotypes are fairly straightforward and well accepted, some extensions of this logic are contentious [85]. Here, we consider the special case of collective extended phenotypes produced by multiple, possibly unrelated individuals. Such collective extended phenotypes do not follow the more direct mappings of genotype to phenotype discussed in the main text. Nevertheless, they can have profound, community-wide effects on climatic conditions and those effects emerge from the collective actions of the individuals comprising those communities, with consequences for all community members (ecosystem engineering). The evolutionary trajectories of such traits may reflect 'diffuse evolutionary processes' such as those commonly invoked in coevolutionary theory.

In temperate regions, old-growth forest canopies buffer temperature extremes such that understory air temperatures are lower than atmospheric temperatures during hot periods and higher during cool periods, including in winter [86,87]. Consequently, soil temperature in mature forests is buffered compared with soils in open areas [88]. Thus, the forest canopy and its moderating influences are a collective extended phenotype of the trees and their climatic effects are a form of thermal niche construction (see Figure 1 in main text). These effects are beneficial for many forest-dwelling species [89] and likely also feedback on the performance of mature trees and, hence, evolution.

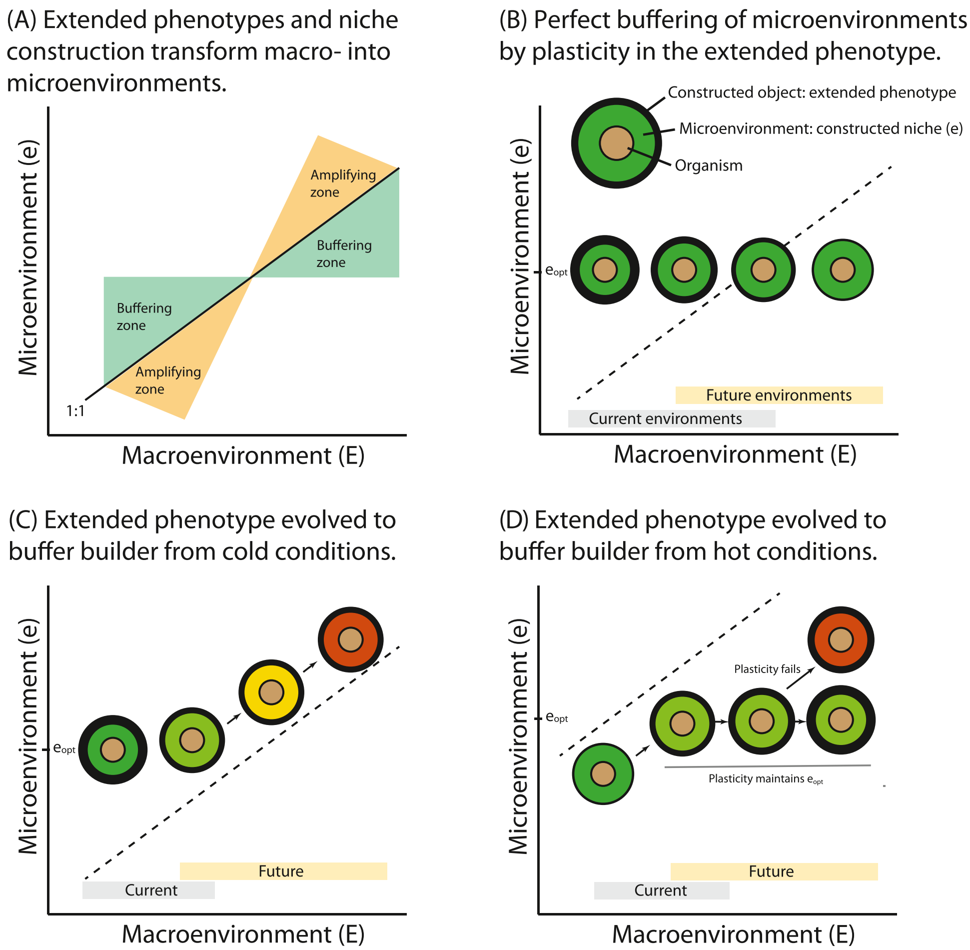
For example, growth rates of fine roots, which are critically important components of carbon cycles [90], depend on soil temperature [91] among other factors. Higher soil temperatures promote fine root growth up to some optimum temperature [92,93], which varies among taxa [91], especially in the superficial soil layers. For mature forest trees, however, the optimal soil temperature usually is lower than atmospheric temperature [94], and even modest warming may slow growth [95]. In addition, in temperate zones, fine root biomass of forest trees peaks in summer [94], when buffering by canopy cover is strongest [86]. We propose that perturbations to canopy cover in summer may, via shifts in soil temperature, have cascading effects on fine root biomass, thereby contributing to the overall response of forest to global change.

Along with other abiotic variables linked to climate change, soil temperature also influences interactions between trees and mycorrhizae [96], which provide many benefits to trees [97]. The net effects of warming on plant–mycorrhizae associations is difficult to predict. In general, climate change appears to have a positive impact on colonization by mycorrhizae [98] but also to alter the dominant types of mycorrhizae (arbuscular versus ectomycorrhizal) associated with trees [99] and soil fungus communities more generally [100]. It remains unclear whether global change is directly altering mycorrhizal communities or whether global tree declines are driving the shifts [101].

The mechanisms by which extended phenotypes of mature trees influence forest floor thermal processes remains poorly documented, yet the thermal buffer should combine with other facilitating processes linked to soil structure, for instance. What is needed now are integrative studies that connect the buffering ability of forest canopies, soil temperature patterns, root performance across soil temperature patterns, and mycorrhizae–tree interactions in their natural thermal contexts in the field. A recent global analysis of forest buffering ability [87], and current calls for large-scale monitoring of soil temperatures [88], are key points of entry for integrating the extended phenotypes of trees into the biology of climate change.

filtering out high-frequency fluctuations and therefore short-term extremes in macroclimatic conditions. Thus, for example, large bird nests or insect mounds often heat and cool slowly enough that their inhabitants escape daily extremes. Larger structures also allow for more complex internal plumbing that can facilitate air movements used to stabilize temperature or ventilate gases (e.g., in bee hives or termite mounds) [31]. Such advantages, however, can disappear on longer time scales: the larger thermal inertia of large structures may trap inhabitants in high heat conditions as average temperatures continue to climb. In addition, organisms with larger or more elaborate extended phenotypes give up freedom of movement and scope for plasticity via behavioral flexibility. Lastly, heat tolerance interacts with body size in complex ways. In general, small animals are more resistant to short-term heat extremes but less resistant to long-term exposure [32] and acclimation capacity typically increases with body size [33]. Consequently, size directly modifies an organism's experience of climate [17] and sets the bounds within which the organism can modify that experience using behavior and physiology.

Second, how much a structure amplifies or buffers its residents (Figure 2A) will depend on how it alters components of their heat budgets [34], including conduction, radiation, convection, and



Trends in Ecology & Evolution

Figure 2. Plasticity of extended phenotypes and consequences for selection. (A) Organisms experience microclimates (e) stemming from extended phenotypes, which are influenced by, but often quite different from, local macroclimates (E). Extended phenotypes can amplify or buffer variation in local climates, with many possible patterns. (B) Round symbols represent individuals (central circle, light brown) and their extended phenotypes (outer circle, black line), which create local microclimates (with microclimatic temperature coded by color). A possible pattern is perfect regulation of microclimates across a variety of macroclimates, resulting in no selection on either the extended phenotype or on internal traits if plasticity can readily compensate for future climates. (C) An extended phenotype that warms individuals during cold conditions. Although such a structure may be effective across historical or current climates, future climates may warm microclimates to levels high enough to cause direct injury or indirect effects via, for example, depressed fertility. Such an outcome could arise if the structure shows no plasticity (indicated by no change in thickness of outer circle, leading the temperature of the constructed microclimate to rise with external climatic temperature). (D) An extended phenotype that cools individuals during warm conditions. In future environments, pre-existing patterns of plasticity may be extended either with or without evolution of underlying behavioral and physiological mechanisms. If the limits of plasticity are reached in the future, microclimates may shift to higher temperatures. In (C) and (D), selection is likely to act most strongly on the extended phenotype and its plasticity and only secondarily on tolerance traits.

evaporation. Extended phenotypes often are buffering because they are coupled by conduction to much larger, more thermally stable objects (large rocks, tree trunks, or the Earth itself, i.e., underground). As with animal surfaces [35], the color and structure of extended phenotypes have complex effects on radiative exchange. Silk tents built by caterpillars, and also galls, rolled leaves, and leaf mines, may to differing degrees reflect or absorb both solar and long wavelength radiation, altering local microclimates [36,37]. Diverse bird species alter the positioning of nests to manipulate radiative load in relation to latitude, altitude, and season [38] (Table 1). Plovers (*Charadrius melodus*), for instance, ensure that eggs experience cooler temperatures by laying them near white pebbles, which reflect more solar radiation [39]. Bird nest placement and materials also alter convective and evaporative heat exchange (reviewed by [40]; Table 1). Construction materials that maintain high humidity minimize water loss by eggs and also provide evaporative cooling [38], a benefit in the heat but also a potential liability when temperatures fall. For all of these reasons, amplifiers are rather rare in the animal kingdom (Table 1).

Flexible behaviors and the plasticity of extended phenotypes

Broadly speaking, behavior is likely to be a major compensatory process for coping with climate change [41–43]. Because extended phenotypes often (but not always) reflect behaviors of their builders, we expect extended phenotypes to show extensive plasticity in response to local

Table 1. Examples across various taxa illustrating well-known extended phenotypes that shape local thermal environments, many of which also exhibit plasticity

Extended phenotype	Traits	Thermal function	Level of plasticity	Refs
Mammals				
Squirrel nest (*Sciurus vulgaris*)	Quantity and quality of materials	(Cold buffer) Insulation during winter	Unknown	[70]
Birds				
Blue and great tit nests (*Cyanistes caeruleus*, *Parus major*)	Mass, insulative properties	(Cold buffer) Insulation from cold	Heavier, better insulated nests in cold	[77]
Open nest of yellow warbler (*Setophaga petechial*)	Size, quantity of material	(Cold buffer) Insulation from cold	Larger nests in arctic versus temperate zones	[78]
Roofed nest of zebra finches (*Taeniopygia guttata*)	Number of strings in nest	(Cold/heat buffer) Insulation property: maintains nest T[a] within narrow range	Fewer strings at elevated T to decrease insulation	[28]
Ground nest of piping plovers (*Charadrius melodus*)	Optical properties of materials	(Heat buffer) Reflective materials provide cooler nest for eggs	Unknown	[39]
Reptiles				
Burrow of tortoise (*Gopherus polyphemus*)	Depth of burrow	(Heat buffer) Insulation from heat	Unknown	[79]
Insects				
Mound of termites (several species)	Morphology: volume, sphericity	(Cold/heat buffer) Insulation from both cold and heat	Construction adjusted depending on internal T	[80]
Hive of honey bees (*Apis mellifera)*	Self-shielding of the workers	(Heat buffer) Insulation from heat	Limit overheating of the honeycomb by increasing the number of workers at its surface	[81]
Tent of *Thaumetopoea* caterpillars (*T. pityocampa*)	Thickness of silk tent	(Cold buffer) Heat absorption to keep winter nest warm	Thicker tents generate higher internal T	[82]
Tent of *Eriogaster* caterpillars (*E. lanestris*)	Thickness of silk	(Cold/heat buffer) Insulation from solar energy to better regulate nest T	Thicker tents provide better thermoregulatory control	[36]
Leaf mine of the apple tentiform leaf miner (*Phyllonorycter blancardella*)	Optical property of surface and lower transpiration	(Heat amplifier) Provides warm environment when exposed to radiation	Unknown	[69]
Burrows of dung beetles (*Onthophagus* sp.)	Depth of burrow	(Heat buffer) Burrows provide cooler, more stable thermal environments	Insects dig deeper to avoid overheating	[83]
Other arthropods				
Burrow of scorpions (family Scorpionidae)	Depth, shape, volume, size	(Heat buffer) Burrows provide cooler, more stable thermal environments	Unknown	[84]

[a]Abbreviation: T, temperature.

conditions and cues (Figure 2B). Some of the best examples of behavioral plasticity that underlies niche construction are from termite mounds and bird nests (Figure 1 and Table 1). In Africa, subterranean termite mounds extend well above the ground surface and mound architecture is altered via collective behaviors so that colony temperature, humidity, and gas concentrations remain within narrow ranges [10,44]. In addition, many birds adjust nest design and placement in response to predictable variation in environmental conditions [40,45]. In zebra finches (*Taeniopygia guttata*), however, nest plasticity reflects temperature only during the first reproductive event, with second nests built like the first nests regardless of ambient temperature [28]. Thus, although some extended phenotypes clearly are modified by behavioral plasticity, limited data preclude generalizations about whether behavioral plasticity will be sufficient to contend with ambient climate warming.

Likewise, the mechanistic roles of plasticity in physiological traits underlying extended phenotypes are seldom documented [46] (Table 1). For example, the silk structures of tent caterpillars interact strongly with incoming radiation [36]. It is unknown, however, whether the temperature history of caterpillars drives plasticity in silk biochemistry or whether local microclimatic conditions alter the properties of extruded silk [47]. Such effects are likely, however, and may have cascading feedbacks on tent temperature. Similarly, the structure of insect galls emerges from crosstalk between insect physiology and plant biochemistry [48]. Gall morphology varies along climatic gradients, raising the possibility that the crosstalk is modulated by temperature [49]. Lastly, plasticity in physiological traits underlying extended phenotypes is likely to be intimately linked to plasticity in behavior: we expect higher physiological plasticity when behavioral flexibility is low and environments vary predictably, such as in sessile organisms (analogous to behavioral versus physiological thermoregulation [46]).

A key problem is to understand how the plasticity of extended phenotypes depends on the **modularity** of the underlying behaviors and physiologies used to construct them. For example, nest-building and other behaviors require a complex sequence of specific behaviors, which may be highly correlated and even traded-off against one another. But, in general, how much are different behaviors in a sequence free to vary? In a rare investigation of this question, Royauté *et al*. [50] found overall no or only weak positive correlations among diverse nest-building behaviors in alfalfa leaf-cutting bees (*Megachile rotundata*). Similar studies across diverse taxa, from divergent climates, are urgently needed to derive generalities about the plasticity (or a lack thereof) of extended phenotypes and any direct or indirect link(s) of these to climate change.

Evolutionary responses of organisms and their extended phenotypes

To examine evolutionary trajectories of organisms and their extended phenotypes, it is useful to divide phenotypes into those internal to the organism, including physiological tolerances, versus the extended phenotype along with the organismal traits responsible for inducing, building, or maintaining it. As climates change, which phenotypes will come under more sustained selection? Which will evolve more readily? The outcome (Figure 2) will depend on whether the extended phenotype is amplifying or buffering, on patterns of plasticity, if any, and on relative levels of genetic variation between internal and extended phenotypes.

For the few extended phenotypes that are amplifiers, novel climatic conditions are likely to generate novel microclimates. These may often be stressful and will lead to selection either on the extended phenotype (selecting for modified construction that provides more suitable microclimates) and underlying patterns of plasticity, or on organismal tolerances (selecting for greater tolerance). The outcome will depend on how radically climate changes and on pre-existing patterns of plasticity. For example, both leaf mines and silk tents likely evolved in part to buffer their builders from cold. As they absorb solar radiation, they warm substantially above air temperature, which can provide critical boosts to rates of feeding, growth, and development. The offsetting risk on hot days, which will occur more frequently with climate warming, is overheating, which we expect to exert strong selection on the builder's upper thermal limits (Figure 2C). In such populations, climate change in effect will drive a change in sign of the primary problem: from too little heat to too much, thereby shifting the buffer into an amplifier. Consequently, these lineages appear unlikely to exhibit adaptive plasticity in construction that could be modified rapidly by strong selection [51], such that selection will fall most strongly on organismal tolerances. The question then becomes whether upper thermal limits have heritabilities high enough to support rapid evolution. Although estimating such heritabilities accurately is difficult, meta-analyses comparing ectotherms, endotherms, and plants suggest substantial conservation of upper limits across taxa [52,53] and only low to moderate heritabilities [54].

For buffering extended phenotypes, by contrast, we predict fundamentally different evolutionary trajectories and more resilience in the face of climate change, at least in the short term. Because the plastic physiologies and behaviors of buffering are already in place, they may be more readily extended by strong selection ([55]; but see [56]) (Figure 2D). Furthermore, some complex behaviors resulting in extended phenotypes have known genetic bases [57] and some extended phenotypes show significant heritabilities [58], as do reaction norms for behavior more generally [59]. We thus predict that selection by extreme climatic events (like high temperatures) will shape primarily the extended phenotype and its patterns of plasticity rather than traits internal to the organism (tolerances). This argument invokes a kind of **Bogert effect** for extended phenotypes, in which behavioral flexibility or plasticity blunts selection on physiology [60,61]. Indeed, a recent meta-analysis compiling data on more than 1000 selection gradients found significantly weaker selection on traits subjected to constructed versus nonconstructed niches [62]. Nevertheless, because climates are changing rapidly [2], buffering capacities may eventually be exceeded, revealing cryptic genetic variation for tolerances. In this sense, buffering extended phenotypes may act as evolutionary capacitors that allow genetic variation in physiological tolerances to build up, which in turn can facilitate rapid evolution, if and when the limits of buffering are reached [63]. These issues lie squarely within a broader discussion about the degree to which plasticity facilitates or inhibits evolutionary change [41,43,55,60,64–66].

Concluding remarks

Since the publication almost 40 years ago of *The Extended Phenotype* [9], the idea of extended phenotypes has gained traction in many areas of biology [10,25]. The concept is stimulating because it blurs the line between genes and environment [67]. By way of extended phenotypes, genes and organisms project their phenotypes into their local environments. In doing so, however, they modify those environments such that the environment becomes an experience that they participate in constructing. In this age of climate change, studies on the roles of constructed microclimates, and how plasticity and evolution can shape them, are critical to resolving whether extended phenotypes will buffer or amplify climate change. Progress will require focused studies on a broad array of interlocking aspects of the biology of extended phenotypes (see Outstanding questions).

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Declaration of interests

No interests are declared.

Outstanding questions

How do extended phenotypes modify the microclimatic experiences of organisms? Several systems have been studied intensively, but broader generalizations depend both on additional comparative work on a much greater diversity of taxa and kinds of extended phenotypes and on studies that reveal general physiological and biophysical mechanisms.

Do the microclimatic niches produced by extended phenotypes alter predictions about organismal resilience, distribution, and abundance obtained from climate models? Recent climate-species models incorporate the specifics of organismal situations, including the effects of local microclimatic conditions and the behavioral responses by organisms. A productive next step would be to incorporate microclimatic niche construction.

How plastic are extended phenotypes in response to climate variability and does plasticity reflect shifts in behavior or physiology? Is plasticity in extended phenotypes adaptive and, if so, under what contexts? Patterns of plasticity in extended phenotypes, and the mechanisms underlying it, are virtually unknown. Future studies should use integrative approaches and should leverage the robust theoretical and empirical frameworks established in other contexts.

How rapidly will extended phenotypes evolve and will selection shape the capacities and tolerances of the organisms themselves or the behaviors and physiologies used to construct extended phenotypes? Answers will require estimating heritabilities of extended phenotypes and the mechanisms underlying them, assessing the strength of selection on these components, and analyzing evolutionary trajectories in related taxa using comparative methods.

Does plasticity in extended phenotypes facilitate or inhibit evolutionary change? In the short term, adaptive plasticity may blunt selection on underlying physiological tolerances. Plasticity, however, also provides coordinated, pre-existing axes of variation that selection may amplify rapidly.

How important are the effects of extended phenotypes on temperature versus on other aspects of microclimates? Extended phenotypes often play multiple roles, including protection from predators, enhanced respiratory gas control, water savings, as well as altering temperatures experienced. A key question is how important temperature effects are compared with others, or how they interact with others, and whether responses to selection imposed by warming climates is constrained by other functions.

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