

## Review

## Metamorphosis in an Era of Increasing Climate Variability

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Most animals have complex life cycles including metamorphosis or other discrete life stage transitions, during which individuals may be particularly vulnerable to environmental stressors. With climate change, individuals will be exposed to increasing thermal and hydrologic variability during metamorphosis, which may affect survival and performance through physiological, behavioral, and ecological mechanisms. Furthermore, because metamorphosis entails changes in traits and vital rates, it is likely to play an important role in how populations respond to increasing climate variability. To identify mechanisms underlying population responses and associated trait and life history evolution, we need new approaches to estimating changes in individual traits and performance throughout metamorphosis, and we need to integrate metamorphosis as an explicit life stage in analytical models.

### Metamorphosis Is an Inherently Vulnerable Life History Stage

Understanding how temporal variability in environmental conditions affects the dynamics of natural populations is a central challenge in ecology and evolutionary biology [1,2]. The importance of disentangling these effects has become even more apparent with worldwide increases in **climate variability** (see [Glossary](#)) [3,4]. Increases in the frequency and intensity of extreme temperature and precipitation events are affecting population dynamics as much as changes in mean climate conditions [5,6]. However, proximate causes and long-term consequences of these population responses remain poorly studied, limiting our ability to assess generality of causal mechanisms and risks to biodiversity.

Most animals have **complex life cycles** that include some form of **metamorphosis** [7,8], a stage during which abrupt ontogenetic changes can make individuals vulnerable to environmental stressors. This group includes insects, amphibians, marine invertebrates, and fishes ([Figure 1](#)), and many of these species have evolved strategies to avoid or withstand environmental variability during metamorphosis. Climate change, however, is likely reducing the effectiveness of adaptations to historical temperature and precipitation regimes, and may pose a particular threat to metamorphic species. To assess this threat, we need to identify proximate mechanisms by which climate variability affects individual survival and **performance** during metamorphosis, and the demographic and evolutionary consequences of those effects.

Metamorphosis entails rapid changes in individual traits and vital rates during a period of potential environmental sensitivity and, therefore, is likely to be an important driver of population responses to climate variability ([Figure 2](#)). Many traits associated with metamorphosis are sensitive to abiotic conditions, including the timing of initiation [9], type and extent of morphological change [10], and – because metamorphosis is metabolically costly – energy status of the individual [11]. These same traits influence the survival, recruitment, and dispersal of pre- and postmetamorphic stages, making metamorphosis a key demographic transition [12–

### Highlights

During metamorphosis and other discrete transitions between life stages, many animals are vulnerable and depend on environmental stability.

As climates continue to change, increasing thermal and hydrologic variability may pose particular risks to metamorphic species, but we lack empirical and analytical resources for assessing these risks.

Many aspects of metamorphosis are sensitive to environmental conditions, including timing and duration, extent of developmental change, and energy costs. Consequently, relative to effects on pre- and postmetamorphic stages, climate variability may have disproportionately strong effects on the traits, fitness, and survival of metamorphosing individuals.

In turn, proximate effects of climate variability during metamorphosis may influence population dynamics and life history evolution by imposing trait and vital rate trade-offs with pre- and postmetamorphic life stages.

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## Trends In Ecology &amp; Evolution

**Figure 1. Metamorphosis and Other Vulnerable Life Stage Transitions Occur across Animal Taxa.** Critical axes of variation include dimensionality and degree of change, its duration, its timing within the organism's life history, and whether the transitional stage is immobile or mobile. Five taxa illustrated here represent a range of these life stage transitions, from

(Figure legend continued at the bottom of the next page.)

## Glossary

**Climate variability:** climates are variable on many time scales, and variability can be both predictable (seasonal shifts) and unpredictable (day-to-day weather). For our purposes, climate variability describes how climate elements such as temperature and precipitation depart from average values in given months, seasons, years, decades, or centuries. In general, climate variability increases as average conditions rise.

**Complete metamorphosis:** also known as holometabolism, a form of insect development which includes four stages: egg, larva, pupa, and adult. Immature, premetamorphic stages of holometabolous insects are very different from the mature, postmetamorphic stages, and the metamorphic pupal stage is largely immobile.

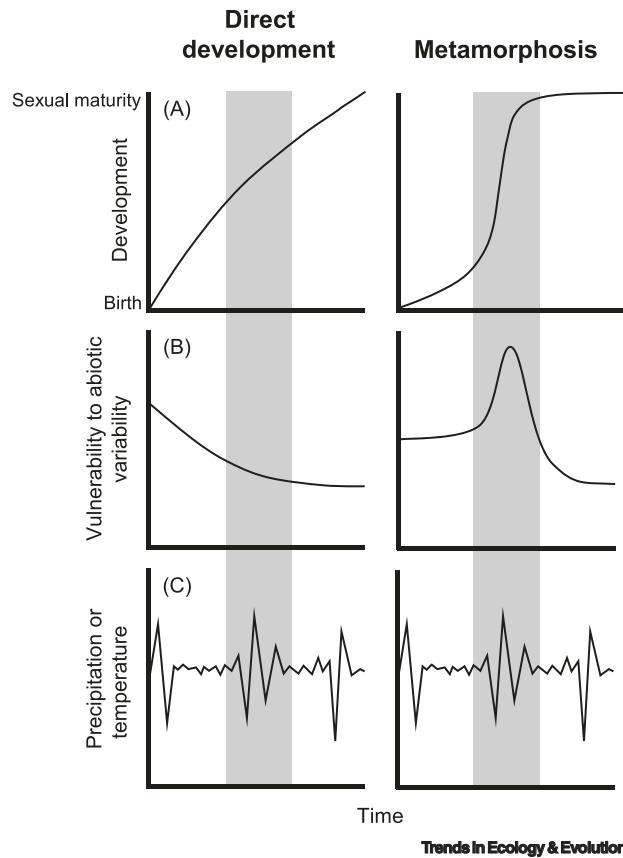
**Complex life cycles:** a life history that includes an abrupt ontogenetic change in an individual's morphology, physiology, and behavior, usually associated with a change in habitat.

**CT<sub>MAX</sub> and CT<sub>MIN</sub>:** upper and lower thermal tolerances, respectively. These are typically defined by ramping temperatures up or down, and identifying the temperature at which organisms lose the ability to perform some function like righting themselves. Measured tolerances typically also depend on technique used to measure them (e.g., rate at which temperature is ramped).

**Heat-hardening response:** process by which exposure to a moderately high temperature induces physiological responses (e.g., induction of heat shock proteins) that subsequently protect the organism from even higher temperatures.

**Incomplete metamorphosis:** also known as hemimetabolism, a form of insect development that includes three stages: egg, nymph, and adult. Nymphs are active and grow gradually through a series of instars (developmental stages between molts) until sexual maturity is reached. The nymph often resembles the adult stage but lacks wings and functional reproductive organs.

**Metamorphosis:** process by which an animal physically develops after birth or hatching, involving a conspicuous and rapid change in body structure through cell growth and differentiation.



**Figure 2. Increasing Climate Variability May Lead to Higher Fitness Costs in Metamorphic Species Than in Direct Developing Species.** Here we assume that rate of developmental change (slopes of the functions in A) increases vulnerability to abiotic variability (B), but recognize that this will not be true for all metamorphic species or under all abiotic conditions. If this is true, however, then climate variability (C) may lead to fitness costs in metamorphic species that exceed those experienced by direct developing species. Shaded areas identify a hypothetical critical time period when high climate variability (C) overlaps with the occurrence of metamorphosis (A). Time scale is defined by the developmental life history of the focal species, which may range from days to years.

**Performance:** here performance is used to refer to nonlethal effects of climate variability during metamorphosis, which may influence fitness (i.e., survival and reproductive capacity) of postmetamorphic individuals.

14]. More broadly, the many trait–vital rate interrelationships established during metamorphosis underscore the potential for significant demographic and evolutionary consequences of climate variability [15,16].

We hope this review shows the importance of quantifying individual survival and performance during metamorphosis, estimating selection on metamorphosis-specific traits, and delineating metamorphosis as an explicit stage in life history analyses. By highlighting the demographic consequences of survival and performance during metamorphosis, this review may also be useful for assessing risks to biodiversity in this era of increasing climate variability. Although we focus on metamorphic species, many non-metamorphic species also experience increased vulnerability during discrete transitions between life stages (e.g., young birds or reptiles hatching from eggs or leaving nests; Figure 1) and many of the concepts here are relevant to those species as well. Likewise, we draw from research on these non-metamorphic species to fill gaps in our understanding of the proximate and ultimate effects of climate variability during metamorphosis (Box 1).

the wholesale morphological and physiological reorganization that occurs during true metamorphosis to more modest ontogenetic transitions, including (from right to left) the Rock Crab (*Cancer irroratus*), the Winter Flounder (*Pseudopleuronectes americanus*), the Wood Frog (*Lithobates sylvaticus*), the Carolina Sphinx (*Manduca sexta*), and the Hermit Thrush (*Catharus guttatus*). Illustration by Bayla Arietta.

## Proximate Effects of Climate Variability during Metamorphosis

Climate variability may affect survival and performance during metamorphosis by physiological, behavioral, and ecological mechanisms. Interactions among these mechanisms are also likely, creating diverse pathways for fitness effects during metamorphosis.

### Physiological Mechanisms

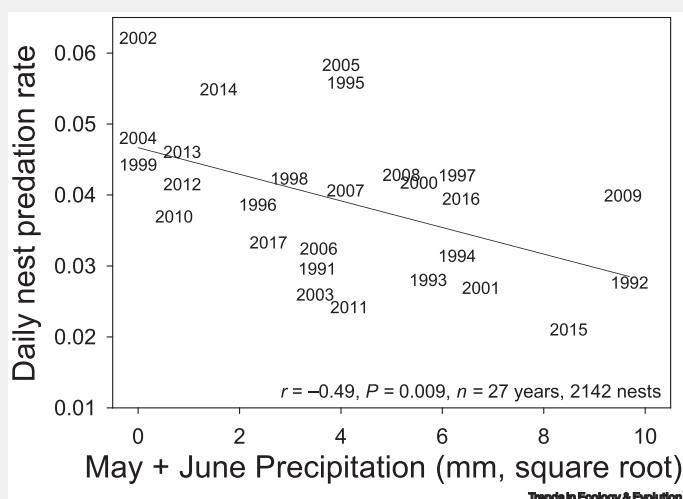
As suggested earlier, metamorphosis likely is a period of vulnerability for most organisms. Physiological systems – including those devoted to sensing, homeostasis, and locomotion – often are radically remodeled during metamorphosis. Consequently, metamorphosing individuals may be inherently less able to withstand abiotic variability than other life stages, both because they may be less capable of mounting strong homeostatic responses to abiotic stress, and because they lack the means to move effectively among locally available mosaics of conditions.

Alternatively, these vulnerabilities may have led to strong selection to withstand the typical stresses associated with metamorphosis. Animals with complex life cycles progress through

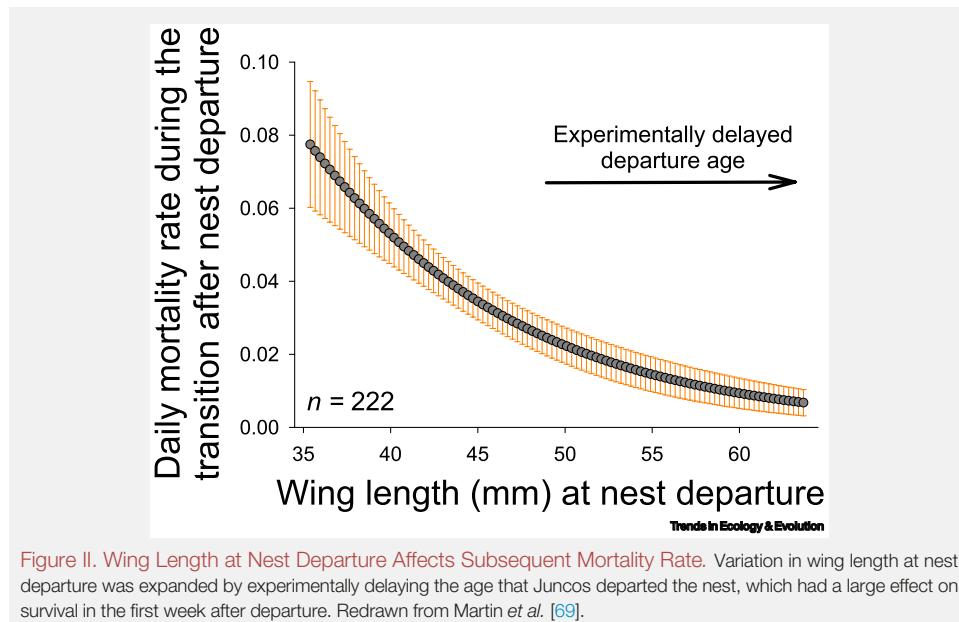
### Box 1. Songbirds Are Vulnerable to Precipitation Variability during Life Stage Transitions

Droughts are expected to increase in frequency and intensity over time [92]. Decreased precipitation can indirectly affect development at life stage transitions in songbirds through effects on nest predation risk. Decreased precipitation is associated with increased nest predation rates [93,94]. For example, average annual nest predation rates of Gray-headed Juncos (*Junco hyemalis*) increased with decreased precipitation during the primary nesting months (May and June) over 27 years, in high elevation riparian forests of Arizona, USA (Figure I).

Parents typically feed young at lower rates when risk of nest predation increases either naturally or with experimental playback of predator sounds [95]. In turn, offspring grow slower (especially wing growth) and often depart the nest at earlier ages when risk is higher [96,97]. Similar to earlier metamorphosis associated with predation risk affecting phenotypic expression, wing development is strongly influenced by departure age and influences flight performance and survival during the initial few days of the transition period after leaving the nest (Figure II) [69,81]. Thus, precipitation has a trickle-down effect through nest predation risk (Figure I) that affects growth and developmental state of young for the transition period after leaving the nest, with consequences for flight performance, and predation rates of these fledglings during the transition after leaving the nest (Figure III).



**Figure I. Nest Predation Rates Vary with Precipitation.** Daily nest predation rates for Gray-headed Juncos (*Junco hyemalis*), in each of the 27 years in high elevation [2350 meters above sea level (m asl)] riparian forest in northern Arizona, USA, increase with decreased precipitation during the nesting season. Sample sizes per year are strong (median = 84 nests  $\text{yr}^{-1}$ ; range = 46–154 nests  $\text{yr}^{-1}$ ; updated from [94]).

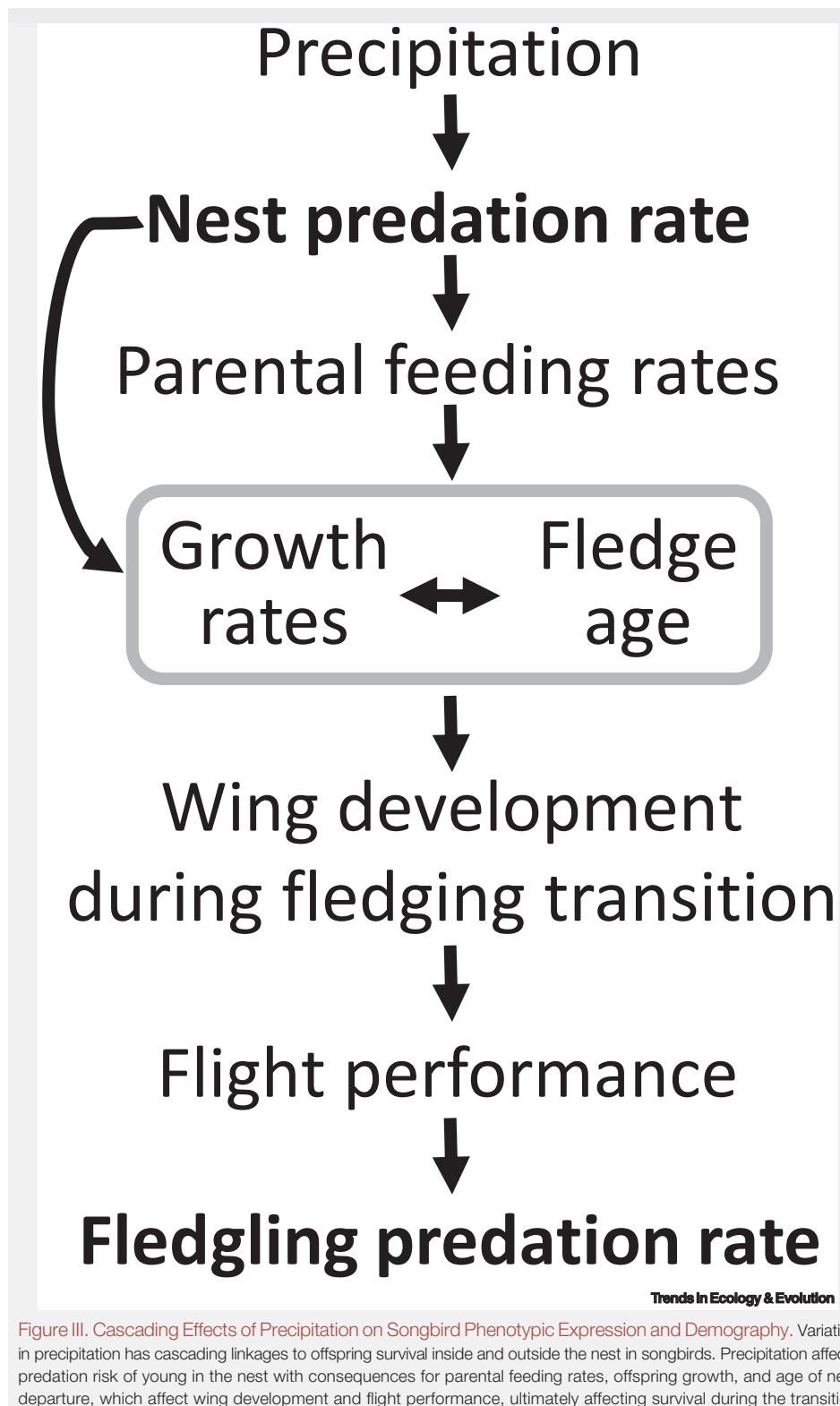


**Figure II. Wing Length at Nest Departure Affects Subsequent Mortality Rate.** Variation in wing length at nest departure was expanded by experimentally delaying the age that Juncos departed the nest, which had a large effect on survival in the first week after departure. Redrawn from Martin *et al.* [69].

and interact with sequences of habitats during their lives, each of which presents a distinct set of physiological challenges [17]. Physiological tolerances may evolve in response to the specific challenges faced by each stage, including metamorphosis. Moreover, in species with immobile metamorphic stages, the lack of ability to move may magnify selection on physiological tolerances, so that it is more frequent or intense than in species with mobile metamorphic stages (Figure 3) [18]. If so, individuals may not be uniformly more or less sensitive to abiotic variability during metamorphosis than during other stages.

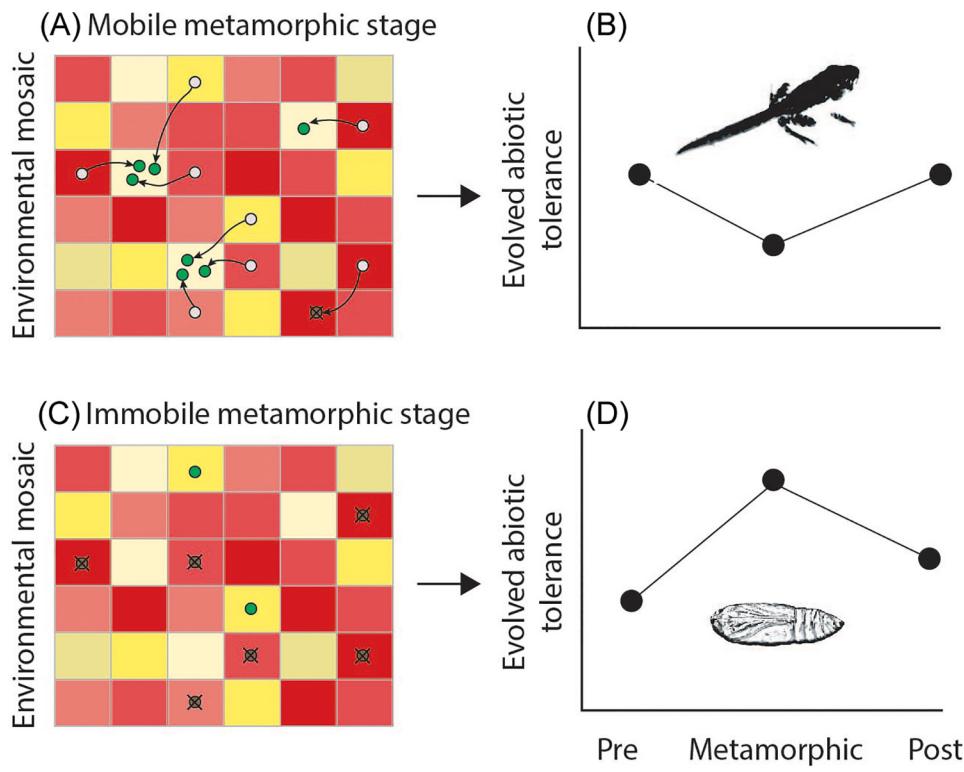
We lack data to distinguish these outcomes unambiguously, but there may be a signal in how different taxonomic groups respond to abiotic extremes during metamorphosis. Studies of amphibians show lower **CT<sub>MAX</sub>** and higher **CT<sub>MIN</sub>** during metamorphosis than during pre- and postmetamorphic stages [19,20]. In addition, metamorphosing American toads (*Anaxyrus americanus*) showed a weaker **heat-hardening response** than tadpoles [21], suggesting that metamorphosing individuals are particularly vulnerable. This is also consistent with the observation that amphibians are generally mobile during metamorphosis, which may allow them to avoid abiotic extremes by exploiting local variation in temperature and moisture (Figure 3).

By contrast, the pupae of insects that undergo **complete metamorphosis** (i.e., holometabolous species) often show higher thermal tolerance than other stages [22,23], and pupae of *Drosophila melanogaster* have the strongest heat-hardening response of all life stages [24]. The contrast with amphibians in evolved tolerances may reflect the immobility of insect pupae, which likely intensifies selection on physiological tolerances. These data also suggest that the remodeling of physiological systems that occurs during metamorphosis is not an insurmountable barrier to evolving high tolerances. Unfortunately, most available data are from studies of temperature; much less is known about insect tolerance of other environmental stressors, including desiccation. Although stage-specific physiological tolerances are gaining more attention, studies remain too sparse to identify strong taxonomic patterns, and explicit analyses of metamorphic stages are particularly needed [25].



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**Figure III. Cascading Effects of Precipitation on Songbird Phenotypic Expression and Demography.** Variation in precipitation has cascading linkages to offspring survival inside and outside the nest in songbirds. Precipitation affects predation risk of young in the nest with consequences for parental feeding rates, offspring growth, and age of nest departure, which affect wing development and flight performance, ultimately affecting survival during the transition period from inside to outside the nest.



**Figure 3. Differences in Evolved Physiological Sensitivity during Metamorphosis Depending on Mobility.** (A) In species that remain mobile during metamorphosis, like many amphibians, individuals may be able to choose among conditions within local environmental mosaics and thereby minimize exposure to harsh conditions that would exert strong selection on physiological tolerances. (B) In these cases, we might expect that abiotic tolerances will be relatively low. (C) In species that are immobile during metamorphosis, like many holometabolous insects, individuals cannot relocate during metamorphosis in response to local extremes in conditions. Instead, they depend on the preceding stage choosing suitable locations, which may not always be possible to anticipate. As a result, physiological systems are more often subjected to strong selection, (D) potentially leading to the evolution of higher abiotic tolerances.

#### Behavioral Mechanisms

Organisms use a wide range of behaviors to reduce exposure to abiotic variability during metamorphosis, many of which are undoubtedly canalized to ensure successful metamorphosis under historical climate regimes [26]. But we generally expect behavioral traits to be more plastic than physiological or morphological traits [27], especially if those behavioral traits are not directly affected by metamorphosis [28]. Consequently, changes in behavioral traits associated with metamorphosis may be early indicators of species response to increasing climate variability [29].

Choice of pupation and emergence sites by insects exemplifies the importance of behavior in mediating exposure to abiotic variability. In holometabolous insects, choice of pupation site – whether by the individual or the parent – is often based on temperature and hydrologic conditions, and the likelihood that conditions will remain stable throughout pupation is clearly part of this decision [30]. For example, many species pupate in sites buffered from ambient climatic variability, such as deep in the soil, inside living and dead trees, and in hives [31,32]. These behaviors are roughly analogous to choice of emergence sites by hemimetabolous insects – those that undergo **incomplete metamorphosis** – which are also selected to optimize thermal and hydrologic conditions while avoiding extremes [33]. Currently, we have little

basis for predicting whether changes in pupation and emergence site selection can keep pace with increasing climate variability, and whether microhabitat availability will accommodate these behavioral shifts.

Mobile metamorphic stages may move among microhabitats to reduce exposure to climatic variability, but these strategies must be balanced against other behavioral demands (e.g., foraging and predator avoidance) while undergoing developmental changes that often limit behavioral scope [34]. For example, in ectothermic metamorphic species, movement may be used to track optimal temperatures, using the extrinsic environment to compensate for developmental constraints on behavior during metamorphosis [35]. But if movement rates increase to track optimal thermal conditions as ambient temperatures become more variable, energetic demands and ecological risks will also increase [36].

#### Ecological Mechanisms

Individuals are exposed to a wide range of intra- and interspecific interactions during metamorphosis, and here we consider mechanisms by which climate variability may influence fitness costs of these interactions via direct effects on metamorphic species. Of course, increasing climate variability may also indirectly affect survival and performance during metamorphosis and similar life stage transitions, such as by influencing the abundance and behavior of predators, diseases, and interspecific competitors (Box 1) [37].

In mobile metamorphic stages, the transitional morphologies that occur during metamorphosis are often more susceptible to predation because they are mismatched to both pre- and postmetamorphic habitats. This is the case in amphibians that resorb their tails and grow legs during the transition from aquatic larvae to terrestrial adults, making individuals more susceptible to predation during metamorphosis by reducing escape performance both in water and on land [38,39]. Similarly, many species with immobile metamorphic stages are highly susceptible to predators and parasites during metamorphosis due to the lack of movement capacity [40,41]. As a result, any changes in climate variability that affect the duration of metamorphosis may affect length of exposure to predation risk and cumulative mortality. Although duration of metamorphosis is sensitive to mean temperature and hydrologic conditions [42,43], there is a clear gap in our understanding of the effects of short-term fluctuations in these conditions.

Climate variability may also change characteristics of the extrinsic environment in ways that mitigate or intensify morphological constraints on escape performance during metamorphosis. Even in regions where climate change is reducing mean water availability, extreme precipitation events that saturate terrestrial habitats may allow species transitioning out of aquatic habitats – and escaping aquatic predators – to access terrestrial refuges earlier in metamorphosis [44]. Conversely, short-term fluctuations in temperature may limit access to refuges from predation within aquatic and terrestrial habitats, adding to morphological limitations. For example, many larval amphibians and insects move between open water and shallow littoral zones of ponds to avoid predators and access food before and during metamorphosis [45,46]. But littoral zones are prone to extreme fluctuations in temperature that may make them inhospitable under future regimes of climate variability [47].

In addition to top-down effects of predation during metamorphosis, climate variability will likely influence the strength of intraspecific competition for metamorphosis sites. If availability of sites with consistently optimal thermal or hydrologic conditions declines with increasing climate variability, then competition for those sites will likely increase. This reduction in availability may intensify interference competition if premetamorphic individuals fight for access to optimal sites

[48]. However, regardless of these direct interactions, fewer optimal metamorphosis sites should cause density-dependent reductions in survival or performance during metamorphosis as more individuals are forced into suboptimal sites [49].

#### Interactive Mechanisms

Climate variability will rarely affect survival and performance during metamorphosis by just one of these mechanistic pathways, as is clear in the examples provided. Indeed, particularly strong and wide-ranging effects will likely emerge from interactions between physiological, behavioral, and ecological mechanisms. For example, in diverse communities dominated by metamorphic species, such as pond-breeding amphibians or stream macroinvertebrates, we would expect high interspecific variation in physiological tolerance to increasing climate variability, resulting in similarly high variation in effects on mortality, abundance, and phenology. Ultimately, species-specific responses have the potential to alter existing interspecific interactions, eliminate some interactions entirely, and create novel interactions, restructuring community ecology and resulting patterns of species diversity.

Interactions between physiological and behavioral mechanism may have evolutionary effects stemming from tradeoffs between mobility and tolerance (Figure 3). For example, if climate variability exceeds the physiological tolerances of holometabolous pupae, selection may act to reduce the duration of immobility, thereby potentially constraining the biological complexity of postmetamorphic stages [50]. A wholesale transition from complete to incomplete metamorphosis is unlikely in insects, where incomplete metamorphosis is ancestral [51]. But such 'reverse' life cycle shifts have been documented in salamanders, where the ancestral, biphasic life cycle has re-evolved within lineages with direct development, a derived life cycle [52]. Salamanders have also independently evolved paedomorphosis numerous times, a life cycle in which metamorphosis is absent or incomplete, and the aquatic larval morphology and ecology are retained into adulthood. The evolution of paedomorphosis is often attributed to characteristics of pre- and postmetamorphic environments (e.g., stable aquatic habitats surrounded by hostile terrestrial habitats) [53]. However, paedomorphosis and direct development may also be evolutionary responses to environmental risks during metamorphosis, such as those posed by increasing climate variability.

#### Emergent Consequences of Climate Variability during Metamorphosis

Here we address three key questions underlying the broader ecological and evolutionary consequences of increasing climate variability during metamorphosis: (i) How will changes in survival and performance during metamorphosis affect population dynamics? (ii) What is the scope for adaptation to increasing climate variability by metamorphosis-specific traits? (iii) How do metamorphosis-specific traits trade-off with traits of pre- and postmetamorphic stages to affect lifetime fitness and life history evolution?

#### Demography

To understand how increasing climate variability will affect the long-term persistence of species with complex life cycles, we need to understand how survival and performance during metamorphosis contribute to population dynamics (Box 2). In stage-structured population models, measures of sensitivity and elasticity estimate contributions of individual vital rates to population growth, where sensitivities assess additive contributions and elasticities assess proportional contributions [54]. Although adding a metamorphic stage between pre- and postmetamorphic stages is simple enough, the challenge lies in collecting data on survival and performance during what can be a very brief period of an organism's life when it may be doing its best to remain undetected.

It is common practice to estimate vital rates for specific life stages, or for finer categories when stages encompass multiple size or age classes [54]. However, the survival rate of the final

premetamorphic stage is also commonly estimated based on the probability of recruitment into the first postmetamorphic stage. As a result, survival during metamorphosis is not differentiated from survival during the last premetamorphic stage. To overcome this limitation, we need to explicitly delineate the period of metamorphosis and to estimate survival during that period. Generally, this will demand higher sampling resolution than traditional stage-based analyses require, and observable criteria for detecting the onset and completion of metamorphosis [55].

In addition to the direct demographic effects of survival during metamorphosis, conditions experienced by an individual during metamorphosis can affect vital rates of postmetamorphic stages. Such carryover effects have typically been studied by estimating how environmental factors and associated indices of performance before metamorphosis (e.g., body condition, energy status, and rates of growth or development) influence performance and vital rates of postmetamorphic individuals [56,57]. However, carryover studies have not focused on metamorphosis specifically, so carryover effects attributed to environment and performance before metamorphosis may be partly or wholly the product of environment and performance during metamorphosis [58].

The remedy requires partitioning metamorphosis into its own stage, and then differentiating carryover effects originating during premetamorphic stages from those originating during metamorphosis itself. Similarly, to isolate demographic consequences of metamorphosis-specific carryover effects, study designs must allow researchers to correct for contemporaneous (i.e., noncarryover) sources of variation in postmetamorphic survival and reproductive capacity. This effort will be challenging and will need to be carried out in a diversity of species to gain a thorough understanding of how conditions during metamorphosis contribute to the population dynamics of organisms with complex life cycles.

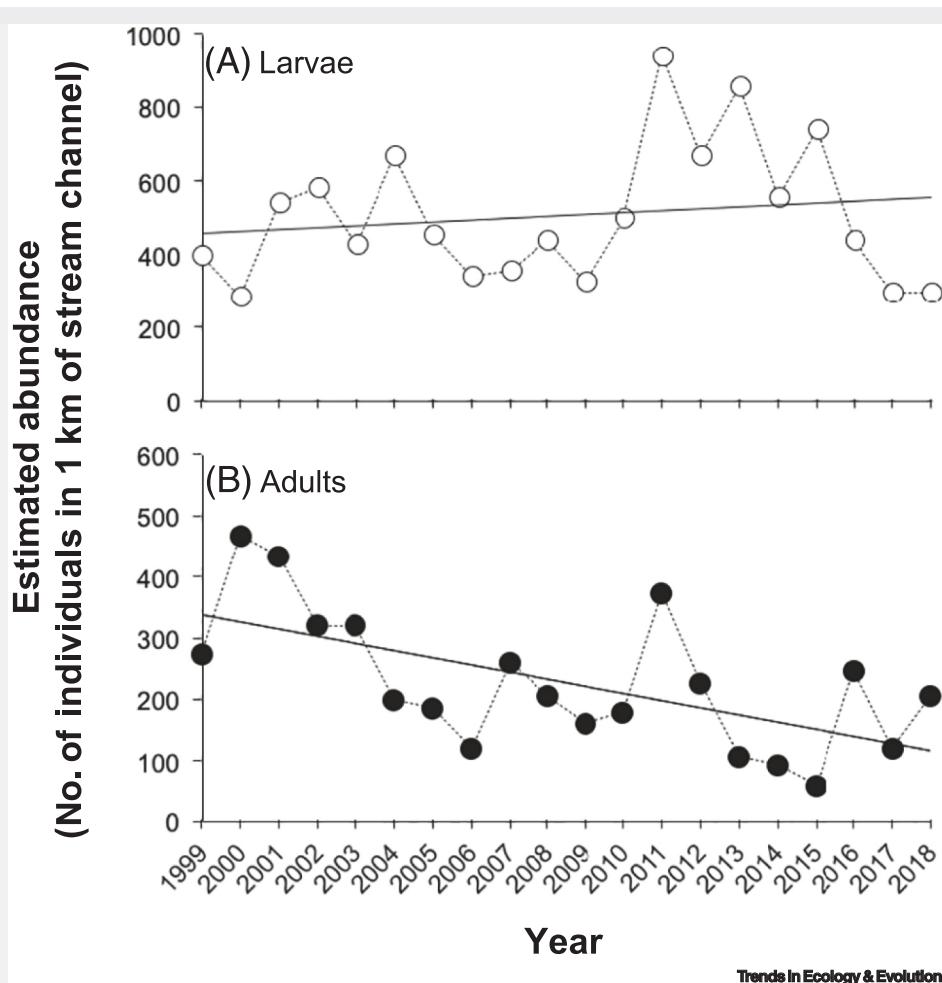
#### Box 2. Streamflow Variability Reduces Survival through Metamorphosis in Salamanders

Changes in variability of precipitation and streamflow are occurring worldwide and likely to have strong effects on freshwater biodiversity. The northeastern USA is experiencing increased annual precipitation, reduced snow cover, and more frequent and intense extreme precipitation events [98], all of which are increasing hydrologic variability. Stream-breeding amphibians may be particularly vulnerable to these hydrologic changes because many are restricted to stream channels during prolonged larval and metamorphic stages.

We used 20 years of data from Merrill Brook, a stream in northern New Hampshire, USA, to understand demographic effects of hydrologic variability on the stream salamander *Gyrinophilus porphyriticus* [99]. Larvae are exclusively aquatic and have external gills which are resorbed during metamorphosis. Postmetamorphic adults rely on cutaneous respiration and remain highly aquatic, but can also be found on land along the stream channel.

Increasing streamflow variability is associated with a long-term decline in the number of *G. porphyriticus* adults in Merrill Brook. Abundance of adults declined by approximately 50% since 1999, whereas the abundance of premetamorphic larvae did not decline (Figure 1). This trend in adult abundance could be caused by a decline in adult survival, but larval and adult survival were constant across years [100]. Instead, metamorphosis appears to be the key stage underlying the decline by influencing the recruitment of new adults.

The probability of survival through metamorphosis declined with increased streamflow variability during summers (June 1 – August 31), when salamanders are active in and along streams (Figure 1). One possible explanation for these results is the inability of metamorphosing individuals to access refuges during low and high flows. Small larvae can burrow deep into the streambed to avoid high flows and access subsurface water during low flows, but the large body size of metamorphosing individuals likely limits access to these deep refuges. Adults can move to streambank refuges to avoid high flows and access moist microsites during low flows [44], whereas metamorphosing individuals are likely restricted to the stream channel due to continued dependence on external gills. Thus, metamorphosing individuals have a unique combination of traits – both morphological and physiological – that may increase their mortality risk under more variable streamflow regimes.

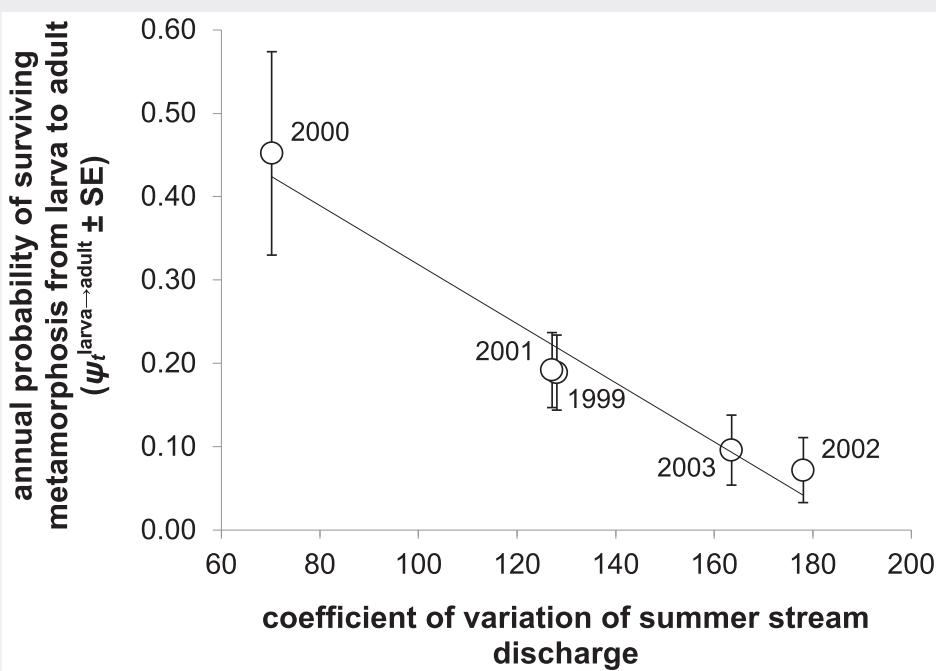


**Figure 1. Long-Term Trends in *Gyrinophilus porphyriticus* Abundance.** Detection-corrected estimates of abundance of larvae (A) and adults (B) in Merrill Brook (1999–2018). Abundance estimates are based on surveys in mid-July. There is no trend in larval abundance ( $n = 20$ ,  $\tau = 0.07$ ,  $P = 0.67$ ), but adult abundance has declined significantly ( $n = 20$ ,  $\tau = -0.45$ ,  $P = 0.01$ ). Redrawn from Lowe *et al.* [99].

### Trait Adaptation

Faced with increasing climate variability, many species will persist over the long term only if there is scope for adaptation of metamorphosis-specific traits. Specifically, survival and performance through metamorphosis may be a function of phenotypic traits that reduce exposure to or increase tolerance of climate variability. Traits that reduce exposure typically will be those associated with finding and using climatic refuges. By contrast, traits that increase tolerance will be those associated with enhanced storage of energy and materials, and specific physiological adaptations for withstanding fluctuations in thermal and hydrologic conditions.

Refuges that reduce exposure to climate variability during metamorphosis may be independently occurring (e.g., sites deep in the soil) or constructed (e.g., pupal chambers). Phenotypic traits may increase the accessibility or effectiveness of such refuges through physiological, morphological, or behavioral mechanisms. For example, morphological traits of the pupal case may dampen abiotic



**Figure II. Streamflow Variability Reduced Survival through Metamorphosis.** The relationship between coefficient of variation (CV) of summer discharge and annual larva→adult transition probabilities ( $\psi_t^{\text{larva} \rightarrow \text{adult}}$ ) in Merrill Brook, New Hampshire, USA. Transition probabilities, estimated from intensive capture-mark-recapture surveys in 1999–2004, represent survival through metamorphosis. Summer discharge CVs were based on mean daily discharge values from a gauge station on the Dead Diamond River, 9.2 km downstream of the Merrill Brook confluence. Point labels are years. Redrawn from Lowe *et al.* [99]. Abbreviation: SE, standard error.

fluctuations experienced by the individual [31,59], and individuals may select stable microhabitats for metamorphosis [60,61]. Unlike traits that reduce exposure, traits that increase tolerance may influence the phenology of metamorphosis – and thus broader life history – as well. For example, if energy reserves increase performance during metamorphosis – a metabolically costly process – selection should favor initiation of metamorphosis when energy reserves of the premetamorphic stage are high [62]. By linking metamorphosis to energy reserves, a plastic physiological trait, this strategy will also affect the timing of metamorphosis, a phenological trait.

Past selection clearly has shaped many metamorphosis-specific phenotypic traits, but several key gaps in knowledge make it difficult to predict whether future adaptive change will keep pace with increasing climate variability. First, metamorphosis is uniquely identified with rapid transformations of many traits simultaneously. Because these transformations often stem from co-occurring developmental processes drawing on common pools of energy and materials, pleiotropic constraints may be especially strong during metamorphosis. If so, the phenotypes of metamorphosis may evolve slowly, even under strong selection imposed by novel climatic conditions [63]. This limitation may be particularly relevant to species with immobile metamorphic stages which often undergo extreme morphological transitions. In these species, increasing climate variability may be more likely to intensify selection on higher-order physiological and behavioral traits (e.g.,  $CT_{\text{MAX}}$  and  $CT_{\text{MIN}}$ , pupal site choice). Second, while the phenology of metamorphosis is already plastic in many species, it is not clear that this plasticity can increase further to accommodate increasing climate variability without incurring fitness costs [64,65].

Finally, and perhaps most fundamentally, although studies have begun to elucidate controls and constraints on phenotype change between pre- and postmetamorphic stages [52,63], we are aware of no study assessing the strength of selection on phenotypic traits during metamorphosis.

#### Life History Evolution

Fitness trade-offs between pre- and postmetamorphic stages shape life histories. Because metamorphosis is rarely treated as a discrete stage, however, we do not know how trade-offs play out across premetamorphic, metamorphic, and postmetamorphic stages. For example, increased mortality of younger age classes can favor reduced reproductive effort, especially when reduced effort enhances future opportunities for reproduction [66–68]. Consequently, increased mortality during metamorphosis could favor reduced reproductive effort. But if parental investment (i.e., per-offspring resources provided by parents) can offset the effects of climate variability on offspring survival during metamorphosis [69–71], reproductive effort may not change but instead be shifted from offspring number to parental investment in offspring quality [72].

The life history implications of parental investment during metamorphosis will depend on the benefits to offspring and the costs to parents in lifetime reproductive success. In some cases, parents might provide direct care to enhance survival during transition phases by reducing exposure to environmental stressors. For example, in fish and insects, some parents enhance offspring survival by mouthbrooding and guarding [73,74], and some frogs transport tadpoles on their backs to water [75]. But mouthbrooding can incur energy costs in parents [76], and egg guarding can inhibit subsequent reproductive attempts [77]. Although these examples do not specifically address metamorphosis, parental care during stage transitions can improve thermal conditions for development, increasing offspring performance and survival [70]. Ultimately, however, to assess the life history implications of increasing climatic variability during metamorphosis, we will need better resolution of parental effects on offspring survival during metamorphosis, and associated costs.

Beyond parental effects, individuals may respond to increasing climate variability by shifting the timing of metamorphosis. Increased mortality risk from warmer temperatures, desiccation, or increases in other mortality sources can all favor younger age of transition to the next life stage [70,78,79]. But such time (age) shifts can also severely impact developmental state at the transition, and depress performance and survival during and after metamorphosis [80,81]. Alternatively, development prior to metamorphosis may speed up to offset these time shifts [82], but little is known about how premetamorphic development interacts with the timing of transition to affect performance and survival during metamorphosis.

Finally, organisms may accelerate the rate of development during metamorphosis, thus reducing the duration of this vulnerable period and avoiding prolonged exposure to climate variability. Faster growth and development, however, may require resources that yield trade-offs in traits that affect performance [80]. In particular, effects of growth and development rates on locomotor traits may influence susceptibility to predation [83,84], but these effects are poorly studied, especially during transition phases. More broadly, although the speed of metamorphosis may reduce mortality during this stage, these benefits must be balanced against any morphological or fitness costs of rapid development in subsequent life stages to predict the ultimate life history implications [69,85].

#### Concluding Remarks

In many species, metamorphosis is difficult to observe because it occurs rapidly and often in refuges difficult for human observers to access. Therefore, quantifying the proximate effects of increasing climate variability will require novel methods that allow us to assess abiotic conditions

#### Outstanding Questions

What is the response to selection of metamorphosis-specific phenotypic traits relative to the response of traits not involved in metamorphosis?

What are the functional relationships describing change in survival probability at the onset and completion of metamorphosis, and how do these transitional survival responses differ in species with mobile and immobile metamorphic stages?

What are the relative effects on survival and performance during metamorphosis of changes in the magnitude versus frequency of temperature and hydrologic fluctuations – the two components of variability?

Can risks experienced during metamorphosis – such as those that may result from increasing climate variability – lead to the evolution of paedomorphic life cycles, or are fitness trade-offs between pre- and postmetamorphic stages the primary cause of these life cycle adaptations?

Will species with immobile metamorphic stages be more affected by increasing climate variability than those with mobile metamorphic stages due to their limited capacity for behavioral responses to abiotic fluctuations?

What are the contributions of mortality during metamorphosis and carryover effects originating during metamorphosis to widespread declines of insect and amphibian populations?

Will changes in climate means interact with changes in climate variability to affect survival and performance during metamorphosis? For example, will increases in mean air temperature allow for faster rates of metamorphosis in ectotherms, reducing exposure to climate variability?

and individual performance throughout metamorphosis. Even more fundamentally, defining the onset and conclusion of metamorphosis is critical to all analyses described here, but in many species metamorphosis is a continuous process distinguished only by an increase, and subsequent decline, in rates of developmental change. Although universal criteria based on these rate changes are difficult to envision, it is possible to quantify rates of change of specific morphological or physiological indices, thereby allowing objective delineation of metamorphosis – even if the criteria are species-specific.

Advances in noninvasive hormone sampling and morphological analyses of wild populations may be especially useful in delineating metamorphosis and tracking individual performance throughout this period. Metamorphosis is often initiated and terminated by changes in concentrations of key hormones, many of which can now be assayed using nonlethal methods in the field [86,87]. Automated analyses of high-resolution digital images may also allow researchers to detect subtle shifts in rates of morphological change that indicate the onset and conclusion of metamorphosis [88,89]. Finally, with dramatic reductions in the size and cost of technologies for tracking individuals and monitoring vital signs remotely, we may soon be able to assess performance and survival of amphibians, insects, and other small animals throughout metamorphosis [90,91].

Beyond these technical advances, we see a broader need for demographic and life history analyses that incorporate metamorphosis as an explicit stage. This key step will allow researchers to quantify the demographic contributions of individuals during metamorphosis, as well as fitness trade-offs across premetamorphic, metamorphic, and postmetamorphic stages (see Outstanding Questions). The rapid developmental changes, phenotypic constraints, and novel interactions with the environment experienced during metamorphosis may lead to fitness trade-offs distinct from those of pre- and postmetamorphic stages. Assessing demographic and adaptive implications of these metamorphosis-specific fitness trade-offs is fundamental to advancing our understanding of the ecology and evolution of species with complex life cycles.

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