

Resolving the consequences of gradual phenotypic plasticity for populations in variable environments

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Abstract. Phenotypic adjustments following environmental change are ubiquitous, and trait changes arising through phenotypic plasticity often lag behind their environmental stimuli. Evolutionary biologists seeking to understand how adaptive plasticity can evolve have extensively studied this phenomenon. However, the ecological consequences of common features of plastic responses to environmental variability, including gradual phenotypic change (i.e., slower than the pace of environmental change), are underappreciated. We present a framework based on the unifying concept of phenotype \times environment performance landscapes that encompasses gradual plasticity. Then, we experimentally investigate the environmental contexts where gradual plasticity is important, using freshwater phytoplankton populations exposed to thermal variation. Finally, based on our conceptual framework, we develop a mathematical model of gradual plasticity that explains population dynamics in variable environments better than common alternative models. Understanding and accounting for the ecological effects of plasticity in variable environments is critical to making vital predictions and advancing ecology.

Key words: acclimation; ecological forecasting; environmental variation; gradual plasticity; performance landscapes; phenotypic plasticity; phytoplankton; Reed Lake; temperature.

INTRODUCTION

A comprehensive understanding of ecology requires discovering how ecological processes unfold in variable environments. Progress towards tackling this grand challenge has been made by studying populations with static trait values in constant environments (Scudo 1984), static trait values in variable environments (Vasseur et al. 2014, Bernhardt et al. 2018), and, more recently, evolving traits in variable environments (Thompson 1998, Hairston et al. 2005, Post and Palkovacs 2009). However, a key means by which organisms change in response to their environment, phenotypic plasticity, has not been thoroughly integrated into this work (Miner et al. 2005). Research in one area is particularly lacking: gradual plasticity. Ecologists commonly assume plastic trait changes keep pace with their environmental drivers (Miner et al. 2005, Forsman 2015, Hendry 2016), yet recent observations show phenotypic changes may be slow enough to interact with environmental change, giving rise to complex dynamics and unexpected outcomes

(Chevin et al. 2010, Cortez 2011, Kremer et al. 2018, Rescan et al. 2020). The extent to which these gradual plastic responses occur across different taxa, systems, and mechanisms of plasticity remains largely unknown, yet critical to resolve. The ubiquity of phenotypic plasticity and environmental variability suggests the phenomenon may be broadly significant. Without a nuanced integration of phenotypic plasticity into ecology, efforts to understand the dynamics of variable ecosystems will be hindered. This inevitably limits our ability to control invasive species, anticipate emerging diseases, conserve natural resources, and manage biodiversity loss in an era of dramatic environmental change.

Phenotypic plasticity can have significant effects on the ecology of populations and communities via several mechanisms. These act over a range of timescales and levels of biological organization (e.g., molecular, physiological, developmental, or behavioral responses) (Feder and Hofmann 1999, Forsman 2015, Donelan et al. 2019) and include reversible responses occurring within an individual's lifetime (Schulte et al. 2011) as well as changes that span generations (Donelson et al. 2012, Munday 2014). Prior studies integrating plasticity with ecology have primarily investigated how plasticity affects the range of conditions individuals can tolerate and assumed either that phenotypes are fixed at the

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individual level (e.g., developmentally) or change very rapidly (i.e., the current environment perfectly describes the current phenotype), and enhance performance (Miner et al. 2005). Nascent theory suggests plasticity may expand species ranges (Berg and Ellers 2010), expedite colonization and invasion success (Richards et al. 2006, Davidson et al. 2011), and stabilize population dynamics in changing environments (Miner et al. 2005, Chevin et al. 2010). At the community level, theory is equivocal: coexistence can be either promoted (Křivan 2003, Miner et al. 2005) or inhibited (Kremer and Klausmeier 2013) by plasticity, depending on elusive details like generalist–specialist trade-offs (Abrams 2006). Limited empirical evidence hints at plasticity’s ecological importance. For example, invasive plants are often more plastic than natives (Davidson et al. 2011), but plasticity can mitigate responses to invasive species (Grosholz and Ruiz 2009). Plasticity can also aid coexistence (Ashton et al. 2010) by favoring resource partitioning among species (Pfennig et al. 2006) and divergent responses to environmental cues (Bernot et al. 2006).

These studies commonly assume that plastic phenotypic change occurs instantaneously; this may severely limit their application when environmental conditions vary on the same timescale as phenotypic change. Many of these studies employ performance curves, which define relationships between physiological, demographic, and ecological traits and environmental variables such as temperature, rainfall, or pH (Kingsolver 2009, Schulte et al. 2011; Fig. 1b). Applications of these relationships generally assume plasticity is instantaneous (e.g., traits perfectly track the environment). Although this is a convenient simplification, plastic changes may often be gradual, lagging behind environmental change (Kronholm and Ketola 2018, Rescan et al. 2020). Gradual plasticity leads to mismatches between an organism’s traits and its environment that affect performance. It can arise through phenotypic changes that are slow and continuous or abrupt, but delayed. For example, the overexpression of many *Saccharomyces cerevisiae* genes occurred >1 h after a single heat shock (Mühlhofer et al. 2019). Biochemical and behavioral responses (Gagliano et al. 2014) may occur quickly relative to physiological

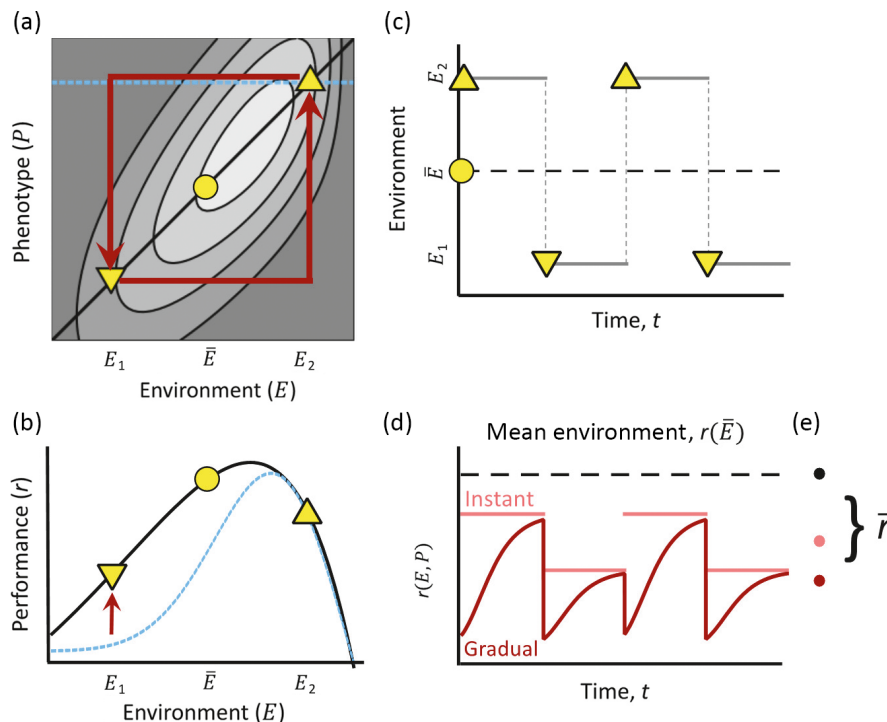


FIG. 1. The consequences of gradual plasticity for population dynamics. Performance landscapes (a) characterize how an individual’s performance (gray contours) depends on its phenotype and current environment. Phenotypic plasticity drives specific relationships between phenotype and environment (reaction norm, diagonal black line). Slices across this landscape provide performance curves (b): a slice taken along the reaction norm provides the acclimated performance curve (black line), and horizontal slices reveal acute performance curves (e.g., blue dashed line). Environmental variation, such as between two fixed environments (c), moves an individual away from its reaction norm (horizontal lines; a), while plasticity (including acclimation) restores its phenotype to the reaction norm (vertical arrows; a, b). When plastic changes are gradual, an individual may spend significant time away from the reaction norm, with consequences for its instantaneous and time-averaged performance (d and e; dark red) that differ significantly from instantaneous plasticity (d and e; light red) or its performance under the mean environment (d and e; black; yellow circles in a–c indicate the mean environment \bar{E}).

(Chazdon 1988, Sims and Pearcy 1993), morphological, and developmental plasticity (Gilbert 1980, Buskirk and Schmidt 2000), but these still take time to unfold.

Substantial ecological consequences can arise from gradual plasticity due to mismatches between current environment and expressed phenotype (Kremer et al. 2018). For example, predation rates on snowshoe hare populations increase when their molting is misaligned with snow cover (Wilson et al. 2019). Without adequate time to induce antipredator morphological defenses, rotifer populations suffer increased mortality (Gilbert 1980). Not surprisingly, performance curves that assume plastic changes occur on a separate, faster timescale than ecological rates are often a poor predictor of population responses to acute environmental changes (Kingsolver and Woods 2016, Sinclair et al. 2016). Models that allow gradual plasticity to influence ecology fare better (Cortez 2011, Kremer et al. 2018, Kronholm and Ketola 2018, Rescan et al. 2020).

A reliable and mechanistic understanding of the ecology of phenotypically plastic organisms inhabiting variable environments (arguably, most organisms) is limited by two challenges, which we address. First, little is known about how broadly significant gradual plasticity is or in which environments it matters most. Second, theoretical and quantitative frameworks that consider gradual plasticity from an ecological perspective are scarce. We empirically study how plasticity influences freshwater phytoplankton experiencing temperature changes, exploring how historical conditions affect acute performance curves (and exponential population growth). With these results, we develop a novel theoretical approach incorporating gradual plasticity into population dynamics. A second set of experiments highlights the broad range of environmental regimes where population growth cannot be adequately predicted without accounting for gradual plasticity. Our results concern a single, but significant, environmental driver (temperature) and a particular study system (unicellular phytoplankton; ecologically important and an emerging model for studying plasticity [Hofmann et al. 2019, Rescan et al. 2020]). However, gradual plasticity likely affects many systems, drivers, and ecological processes. By developing a foundation for studying gradual plasticity, we intend to advance the study of ecology in variable environments, which is essential to achieving major ambitions in applied and predictive ecology (Petchey et al. 2015), especially as global change alters patterns of variability (Wang and Dillon 2014).

Gradual phenotypic plasticity: A conceptual framework

Phenotypic plasticity occurs when individuals with identical genotypes have phenotypes P that are identical in a shared environment and vary systematically across environments E , a relationship termed a *reaction norm* (which we denote as $P = \phi(E)$; see Fig. 1a). Valid phenotypes may include both very specific, low-level traits

or high-level traits (e.g., specific leaf area or respiration rate) that depend on a suite of lower-level traits (that are seldom measured directly). This phenotype may be described specifically by morphological, physiological, or behavioral changes or by some composite of those changes that underlie more complex traits (e.g., specific leaf area in plants or respiration rate in animals). In such cases the phenotype can be described phenomenologically despite the fact that the contributions of specific processes are unknown. *Gradual plasticity* occurs when phenotypic changes do not keep pace with environmental changes, creating frequent or persistent mismatches between an individual's expressed phenotype and its reaction norm. This can occur given a diversity of environments and plastic mechanisms, including responses that are initiated immediately after a perturbation occurs, but accrue incrementally, as well as responses that are large but only initiated after a delay. Here, and in the main text, we focus on one particular type of plasticity: *acclimation*, or reversible changes in physiology, behavior, etc. Individuals whose phenotype matches their reaction norm in a given environment are considered to be *acclimated*.

To explore the ecological relevance of gradual plasticity, we recognize that the performance r of an individual will depend on both its current phenotype P and environment E . Across a range of possible phenotypic values and environmental states this defines a *performance landscape*, where $r = f(P, E)$ (Fig. 1a; termed adaptive landscapes by Chevin et al. 2010). Slices across the performance landscape provide *performance curves* (Fig. 1a, b; termed tolerance curves in Chevin et al. [2010]). The curve tracking the performance of perfectly acclimated individuals across environments is an *acclimated performance curve* ($r = f(\phi(E), E)$, Fig. 1a, b, black line). *Acute performance curves* represent changes in performance of individuals with a fixed phenotype P^* across environments ($r = f(P^*, E)$, Fig. 1a, b, blue dashed lines). Environmental perturbations experienced by an acclimated individual displace it horizontally on the performance landscape, away from the reaction norm (e.g., Fig. 1a, horizontal lines). Acclimation subsequently shifts the individual's phenotype back towards the reaction norm in the new environment (Fig. 1a, b, vertical arrows). The realized performance of individuals in variable environments will depend on factors including the (1) size and frequency of environmental perturbations, (2) performance landscape geometry, and (3) acclimation rate. Effects will be minimal for small, infrequent perturbations experienced by individuals that either exhibit small amounts of trait change across environments or acclimate rapidly, and have small fitness differences between acclimated and nonacclimated phenotypes for a given environment. Outside of these cases, individuals' phenotypes may perpetually chase their environment, resulting in substantial, cumulative effects on individual performance, population dynamics, and higher-order ecological processes (Fig. 1d, e).

For example, consider a population of asexual individuals that are genetically and phenotypically identical (sharing a reaction norm). Assume the population experiences time-varying environment E and is density independent. As a measure of performance r we focus here specifically on the population's exponential growth rate (w ; Malthusian fitness). Additionally, for simplicity, we assume that we can compress relevant phenotypic changes in response to the environment E into a single dimension. This is reasonable when acclimation is driven by changes in a single dominant phenotype, or results from a linear combination of changes in an underlying set of multiple unmeasured phenotypes (ordination techniques could be used to test this assumption in empirical systems where these changes are readily measured). In the limit of rapid (or “instantaneous”) acclimation the current environment directly determines phenotype ($P = \phi(E)$) and performance ($w = f(\phi(E), E)$, following the acclimated performance curve). Then, change in a population's size N is

$$\frac{dN}{dt} = w(\phi(E), E) \cdot N. \quad (1)$$

Alternatively, if acclimation is gradual relative to environmental change, explicitly modeling phenotypic change may be necessary (rather than assuming $P = \phi(E)$). For example, following the framework of Lande (2014):

$$\frac{dN}{dt} = w(P, E) \cdot N,$$

$$\frac{dP}{dt} = \sigma_E \cdot (\phi(E) - P), \quad (2)$$

where phenotype changes according to acclimation rate σ_E and the difference between P and $\phi(E)$, the acclimated phenotype given by the reaction norm (*sensu* Chevin et al. [2010]). For large σ_E , acclimation becomes effectively instantaneous, Eq. 2 reduces to Eq. 1, and performance is adequately described by the acclimated performance curve, $w = f(\phi(E), E)$ (Fig. 1a, b, heavy black line). When σ_E is smaller, acclimation is gradual, and differences between P and $\phi(E)$ persist, affecting population performance. For example, alternations between two environmental states (Fig. 1c) affects performance over time, driving substantial differences between models assuming instantaneous (Eq. 1; Fig. 1d, light red) and gradual (Eq. 2; Fig. 1d, dark red) acclimation. These also diverge from a naïve prediction based solely on the population's performance in a time-averaged environment (Fig. 1d, black). Incorporating different degrees of complexity, these models make distinct predictions of time-averaged performance in a variable environment (Fig. 1e), highlighting the potential for plastic dynamics to affect ecology.

MATERIALS AND METHODS

Quantifying thermal performance landscapes

We measured performance landscapes for two species of freshwater phytoplankton: *Chlamydomonas reinhardtii* (Chlorophyceae; from E. Litchman, Michigan State University, USA) and *Microcystis aeruginosa* (Cyanophyceae; from UTEX Culture Collection of Algae, University of Texas, USA). Unicellular phytoplankton are emerging as model taxa for understanding the dynamic consequences of phenotypic plasticity because they experience daily environmental variation on the same timescale as their demographic rates (Kremer et al. 2018) and, because they lack soma-germline differentiation, they are prone to both intra- and transgenerational plasticity (Rescan et al. 2020). Following the framework outlined in our conceptual framework, we measured performance landscapes where (1) exponential population growth rate (fitness) was our metric of performance, (2) temperature was our environmental variable, and (3) acclimated temperature served as our phenotype. This last simplification assumes that differences in the physiology of populations acclimated to two different temperatures, reflecting coordinated changes in the low-level traits directly responsible for acclimation at the cellular level (e.g., Gerhard et al. 2019), can be summarized as the difference in temperature between the two populations. In other words, acclimated temperature functions as a univariate proxy for a suite of underlying, challenging to measure, traits that change as populations acclimate to new temperatures. In this framing, the relationship between acute temperature and a phenotype described by acclimated temperature produces a linear reaction norm across the performance surface (Fig. 1b). Measuring a species' thermal performance landscapes provides both its acclimated thermal performance curve (Fig. 1b, black) as well as the acute performance curves of populations previously acclimated to different temperatures (Fig. 1a).

For all experiments, we constructed a set of aluminum thermal gradient blocks (TGBs) with dimensions $0.88 \times 0.29 \times 0.08$ m. Hot and cold water were pumped from water baths through channels in opposite ends of the block, establishing a stable, approximately linear, horizontal thermal gradient. Eight temperature sensors were incorporated into each block, providing real-time monitoring of thermal conditions. Each block contains 27 wells, in a 9×3 configuration with ~ 150 ml of deionized water into which up to six replicate test tubes (glass disposable culture tubes 12×75 mm) can sit, forming a heat-conductive interface between tubes and the surrounding metal. In all cases, culture tubes contained COMBO growth media (Kilham et al. 1998). Wells were individually lit from below, using full spectrum 5-W LEDs (380–850 nm, Shenzhen Chanzone Technology Co., China), using continuous light with a mean photosynthetic photon flux of 10.4 ± 1.04 (mean ± 1 SD)

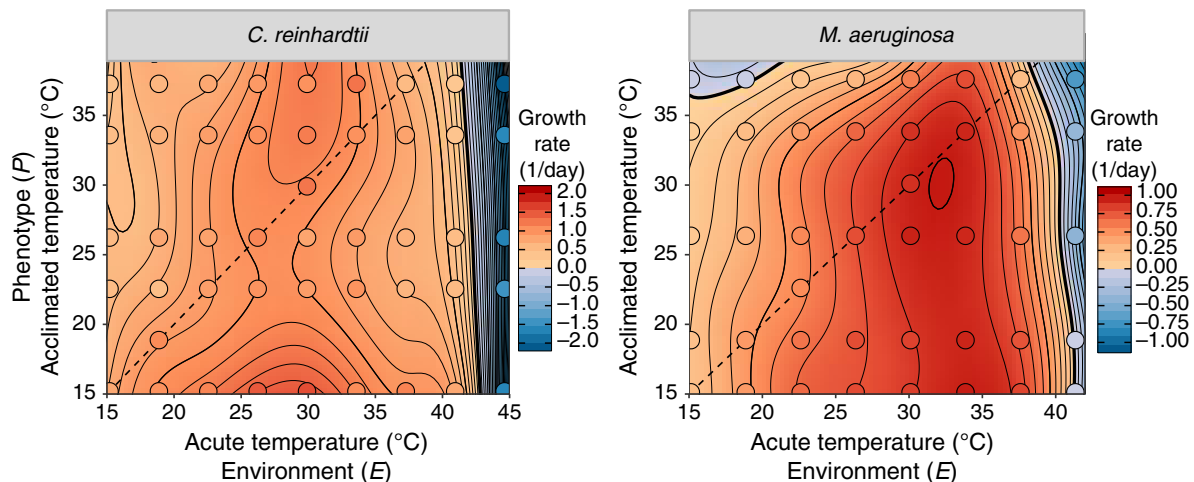


FIG. 2. Performance landscapes reveal the fitness consequences of gradual plasticity. The growth rate of *Chlamydomonas reinhardtii* (left) and *Microcystis aeruginosa* (right) depend on their acclimated temperature (phenotype *P*) and current thermal environment (Environment *E*, both axes expressed in degrees Celsius). Colored surfaces represent growth estimates from generalized additive models fits to measured growth rates (filled circles). Thick black line represents the zero net growth isocline, separating positive (warm colors) from negative (cool colors) growth. Dashed 1:1 line indicates the reaction norm and performance of acclimated populations.

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (see Appendix S1: Fig. S1c for light information).

Prior to measuring the performance landscapes, we acclimated three replicate populations of each species to all nine temperature conditions across the TGBs: 15.3°C, 19.3°C, 22.7°C, 26.4°C, 30.3°C, 33.5°C, 37.8°C, 41.4°C, and 45°C. Cultures were bottlenecked 1 month before starting these assays, then maintained under 24 h light at 21°C (room temperature) and regularly diluted. During the initial acclimation period of at least 2 weeks, cultures were maintained in the exponential growth phase. Ideally, to construct a thermal performance landscape, we would have established a factorial experiment, crossing replicate populations with all nine acclimation histories with all nine possible acute temperatures. This was not logistically feasible. Instead, we simultaneously measured six curves (five acute performance curves and the acclimated performance curve) at nine temperatures, with three replicates per treatment, for a total of 162 populations of each species (see schematic Appendix S1: Fig. S2). For the acute curves we selected populations with five different acclimation histories (Fig. 2 circles): 15.3°C, 19.3°C, 26.4°C, 33.5°C, and 37.8°C (for *M. aeruginosa*) and 15.3°C, 19.3°C, 22.7°C, 26.4°C, 33.5°C, and 37.8°C (for *C. reinhardtii*); these differ in the third temperature to capture anticipated curve shapes based on pilot studies of the two species better. Multiple replicates shared the same well, but temperature and light were tightly controlled to minimize potential well effects (supporting data, Appendix S1: Fig. S1). All populations were inoculated into fresh media with a target starting density of either 20,000 cells/ml (*C. reinhardtii*) or 100,000 cells/mL (*M. aeruginosa*).

To estimate exponential population growth rates, we measured densities fluorometrically four times for each population over a 40-h period, beginning after initial inoculations. Fluorescence was assayed using a chlorophyll-a nonacidification module (Turner Designs, Inc., San Jose, California, USA). We confirmed that fluorescence provided a reliable proxy for cell density (cells/ml) by comparing Raw Fluorescence Units to cell counts obtained using a particle counter (Spectrex PC-2200, Spectrex Corporation, Redwood City, California, USA). These measures were linearly related ($r^2 > 0.99$ for both *C. reinhardtii* and *M. aeruginosa*) over the range of densities that existed during our experiments. This relationship was not influenced by acclimation history for either species as evidenced by three replicate populations with different acclimation histories (15.8°C vs. 35°C) not having significantly different relationships between fluorescence and cell density (*C. reinhardtii* acclimation history \times fluorescence $F_{1,69} = 0.36$, $P = 0.55$; *M. aeruginosa* acclimation history \times fluorescence $F_{1,54} = 2.65$, $P = 0.11$). Finally, we estimated the exponential growth rate of each population as the slope of the relationship between $\log(\text{density})$ and time (calculated in R using the growthTools package;⁶ Appendix S2: Figs. S1 and S2).

Performance landscapes for both species were statistically characterized using generalized additive models (GAMs) to relate exponential growth rate (performance) to acclimation history (phenotype) and acute temperature (environment). Specifically, GAMs were constructed using tensor product smooths of acclimation history and acute temperature with a P-spline basis and fit using restricted maximum-likelihood analysis (to

⁶<https://doi.org/10.5281/zenodo.3634918>

avoid overfitting smaller data sets [Wood 2017]). Alternative GAMs, using different types of bases and numbers of knots were considered using Akaike information criteria (AIC) before selecting this specific model, which performed well for both species. Before model fitting, we excluded observations with acclimation histories $>38^{\circ}\text{C}$, as these populations did not survive. Furthermore, we removed observations for *M. aeruginosa* populations grown at acute temperatures $\geq 43^{\circ}\text{C}$; negative growth rates already occurred at 41°C and quantitative estimates of negative growth rates well outside species' thermal niches are often unreliable. GAM summaries are provided in Appendix S3: Tables S1 and S2.

Developing a quantitative framework for gradual plasticity

We developed three candidate models (see Appendix S4: Table S1) that predict the response of population dynamics to thermal variation, then ran two experiments to test the utility of performance landscapes and determine the domains where gradual plasticity can meaningfully influence population dynamics. First, the simplest model (*mean environment*, Fig. 1d, black) assumes populations grow at the constant, acclimated growth rate corresponding to the time-averaged temperature (arithmetic mean). The second model (*instantaneous acclimation*, Fig. 1d, light red) assumes growth rate changes immediately with temperature, following the acclimated performance curve (as in Eq. 1). This common approach assumes that plasticity occurs instantaneously (Thomas et al. 2012, Vasseur et al. 2014, Bernhardt et al. 2018). The final model (*gradual acclimation*, Fig. 1d, dark red) assumes growth rate depends on both the current temperature and a population's phenotype (represented by acclimation temperature), which may not match their current environment (as in Eq. 2). In this model, populations in variable environments move around the fixed performance landscapes that we previously measured. Changes in temperature displace acclimated populations horizontally from the reaction norm, and the process of acclimation returns populations to new positions along the reaction norm, at a fixed acclimation rate (σ). Although we did not conduct dedicated experiments to estimate this parameter, we were able to estimate its value indirectly for each species. To accomplish this, we used a maximum-likelihood approach to determine the value of σ leading to the closest overall agreement between experimentally observed $\log_{10}(\text{abundance})$ and predicted $\log_{10}(\text{abundance})$, using the gradual acclimation model and assuming normally distributed residuals. For simplicity, we pooled data from two different experiments that manipulated temperature regimes and tracked population growth. Finally, we compared the performance of all three models by considering the correlation of predicted and observed $\log_{10}(\text{abundance})$ for all species and experiments, as well as R^2 , mean absolute error, and AIC comparisons.

Determining environmental regimes where gradual plasticity alters population dynamics

If gradual plasticity is important, and performance landscapes are informative, then populations that have different acclimation histories or experience different environmental sequences (with identical means) should grow differently (see *Predictions made by performance landscapes* in Results). However, gradual plasticity is unlikely to matter in all environments. To explore these ideas, we performed two experiments (using both species) that exposed populations with different acclimation histories to different patterns of temperature variation. Although idealized relative to natural aquatic ecosystems, these environments were deliberately designed to provide clear tests of predictions about when and how gradual plasticity might influence population dynamics.

In the first experiment, populations with two different acclimation histories (cold, 15.3°C , and hot, 37.8°C) were exposed to ascending or descending temperature sequences with identical means (see Fig. 3a for schematic). These consisted of 15.5°C , 22.9°C , 30.3°C , 37.7°C , and 41.3°C , alternating between 16-h and 8-h durations, for a total of 64 h. We used four replicates of each treatment. In the second experiment, populations with a range of acclimation histories (15.7°C , 19.4°C , 23.1°C , and 26.8°C for *C. reinhardtii* and 17.0°C , 20.4°C , 24.0°C , 27.3°C for *M. aeruginosa*) were exposed to fluctuations of six different amplitudes (in steps from 0°C to 19°C). Over 3 d, we manipulated temperatures by manually moving populations along the TGB every 24 h (see Appendix S5: Fig. S1 for schematic). We used three replicates. Populations were inoculated with the target densities described above. Final densities were measured fluorometrically. Neither experiment manipulated the duration of perturbations, although this is also known to matter (Kremer et al. 2018).

Finally, to explore the implications of thermal acclimation for algal populations inhabiting more realistic thermal regimes, we applied our instantaneous and gradual acclimation models to 45 d of hourly surface temperature data from Reed Lake, Portland, Oregon (see Appendix S6: Figs. S1–S3; Data S1: “Predictions for lake env.cdf”). We complemented this with a similar exploration of sinusoidal fluctuations (see Appendix S7: Fig. S1; Data S2: “Predictions for sinusoidal env.cdf”). Both are available as interactive models, manipulating key assumptions, initial conditions, and focal environments.

RESULTS

Thermal performance landscapes

The performance landscapes of *C. reinhardtii* and *M. aeruginosa* indicate substantial impacts of gradual plasticity (Fig. 2). For both species, the temperature populations were previously acclimated to (or

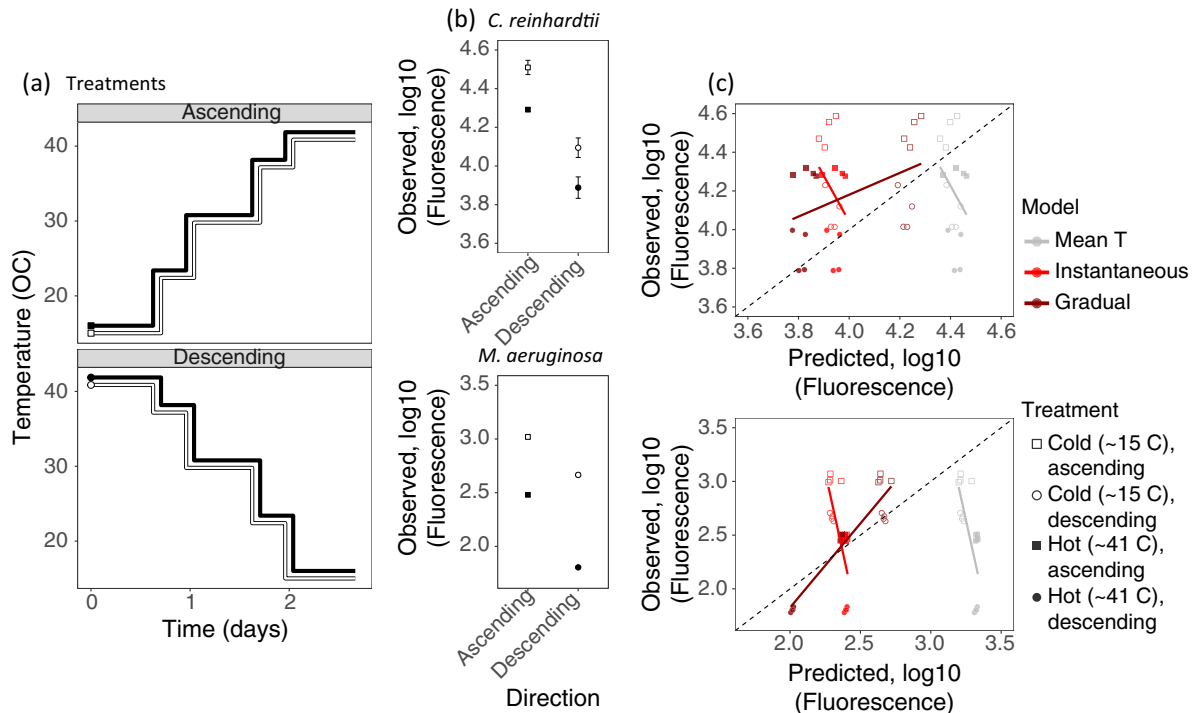


FIG. 3. Time-series data testing the performance landscape's predictions. (a) The initial conditions (cold acclimated [open shapes] vs. hot acclimated [filled shapes]) and asymmetries in temperature variation (ascending [squares] vs. descending thermal environments [circles]) (b) influence final population sizes (means \pm 95% confidence intervals; symbols conceal error bars for *Microcystis aeruginosa*), and as predicted by gradual acclimation (dark red) but not by instantaneous acclimation (red) or mean temperature (gray) models (c). Top row for (b) and (c) show *Chlamydomonas reinhardtii* estimates and bottom row show estimates for *M. aeruginosa*.

acclimated temperature, a proxy for phenotype) influenced acute performance, which diverged from acclimated performance. In some cases, acute performance was lower than in acclimated populations (Fig. 2 dashed 1:1 lines). For example, *M. aeruginosa* acclimated to 34°C and acutely exposed to 15°C underperformed acclimated 15°C populations by 71.0% ($w = 0.066/\text{d}$ vs. $w = 0.227/\text{d}$). In others, acute performance exceeded acclimated performance. *Chlamydomonas reinhardtii* acclimated to 15°C and exposed to 30°C outperformed acclimated 30°C populations by 27.6% ($w = 1.57/\text{d}$ vs. $w = 1.23/\text{d}$). Likewise, *M. aeruginosa* populations acclimated to 15°C and exposed to 34°C outperformed the 34°C-acclimated population by 3.8% ($w = 0.99/\text{d}$ vs. $w = 0.96/\text{d}$). At these acute temperatures, acclimated populations did not yield the maximum performance. Instead, for both species, the highest measured performance across experimental conditions occurred in nonacclimated populations.

Populations acclimated to a lower temperature than their acute environment tended to exhibit enhanced growth (87.10% of instances), whereas populations acclimated to temperatures higher than their acute environment tended to exhibit similar or decreased performance, relative to acclimated populations. This latter impact was particularly evident in *M. aeruginosa*

where populations acclimated to the highest temperature (37.8°C) failed to exhibit positive population growth at the two lowest acute temperatures, unlike the populations acclimated to all other lower temperatures. This instance indicates that the consequences of gradual plasticity can alter zero net growth isocline (ZNGI) boundaries (Tilman 1982).

Predictions made by performance landscapes

These performance landscapes (Fig. 2) make testable predictions for how population dynamics should unfold in temporally variable environments given gradual plasticity (gradual acclimation, Fig. 1d, e dark red). These differ from predictions that assume instantaneous acclimation (Fig. 1d, e, light red) (see *Methods* for model details) or simply average over temporal environmental variation ("mean environment" predictions, Fig. 1d, e, black). Three key predictions are that population dynamics depend on (1) the order of environmental conditions (e.g., warming versus cooling trend), even if mean conditions are identical; (2) initial conditions (e.g., initial phenotype or acclimated temperature); (3) the magnitude of environmental variation. If upheld, these predictions together suggest that across a broad range of temporally variable environments models that acknowledge gradual

plasticity (e.g., gradual acclimation) will outperform models that ignore this feature (e.g., mean environment and instantaneous acclimation; see *Methods* and Appendix S4: Table S1).

Confronting predictions with population-level data

Chlamydomonas reinhardtii and *M. aeruginosa* populations exposed to ascending temperature sequences (Fig. 3a, top) achieved a higher final density than populations exposed to a descending temperature sequence (Fig. 3a, bottom; Fig. 3b, two-way ANOVA for *C. reinhardtii* temporal order, $F_{1,12} = 87.220$, $P < 0.001$; two-way ANOVA for *M. aeruginosa* temporal order, $F_{1,12} = 283.335$, $P < 0.001$). Populations acclimated to low temperatures achieved a higher final density than populations acclimated to hot environments (Fig. 3b, two-way ANOVA for *C. reinhardtii* acclimation history, $F_{1,12} = 27.917$, $P < 0.001$; two-way ANOVA for *M. aeruginosa* acclimation history, $F_{1,12} = 549.427$, $P < 0.001$). By contrast,

neither instantaneous acclimation nor mean temperature models predicted these treatment effects on final density, as all populations experienced the same duration of exposure to different temperatures, and initial abundances were very similar (two-way ANOVA relating initial abundance to acclimated temperature and temporal order was not significant in *C. reinhardtii*, although cold-acclimated populations were seeded with slightly lower abundances in *M. aeruginosa*; $F_{1,12} = 85.43$, $P < 0.001$). These results support predictions 1 and 2. Furthermore, the gradual acclimation model performed better overall than the other models as indicated by a higher coefficient of determination and correlation coefficient for both *C. reinhardtii* and *M. aeruginosa* (Fig. 3c; Appendix S8: Table S1).

A second experiment (Fig. 4; Appendix S5: Fig. S1) tested whether population dynamics were affected by starting temperature (prediction 2) and the magnitude of thermal fluctuations (prediction 3). Overall, the gradual acclimation model improved the accuracy of forecasts across thermal environments relative to the

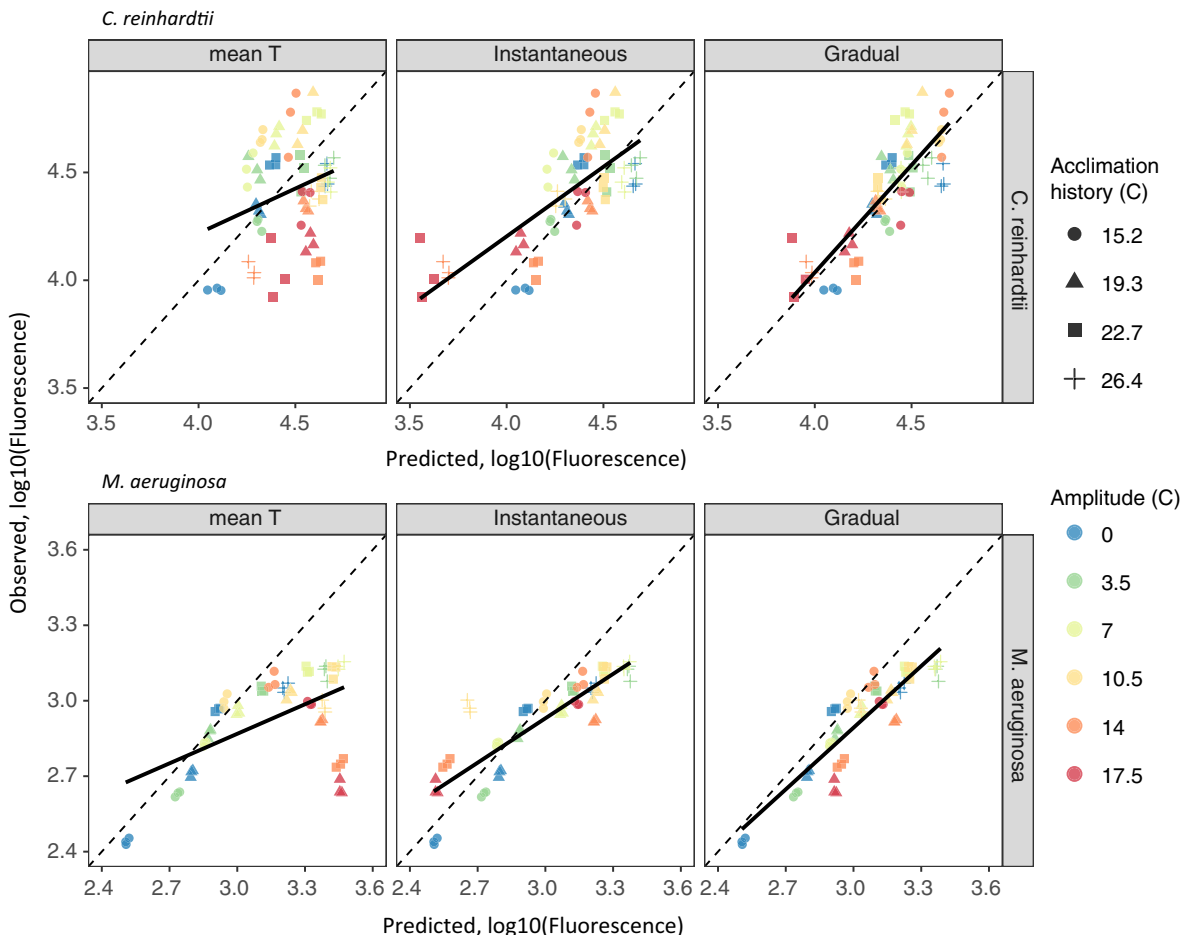


FIG. 4. The observed (empirically measured) versus predicted densities of *Chlamydomonas reinhardtii* (top row) and *Microcystis aeruginosa* (bottom row). Colors indicate which temporal fluctuation phytoplankton populations experienced over 72 h, and symbols indicate their starting acclimation temperature. Columns indicate the use of a mean temperature model (left), an instantaneous acclimation model (center), or a gradual acclimation model (right) to generate predictions.

instantaneous acclimation and mean temperature models, as indicated by a higher coefficient of determination and correlation coefficient, and a lower AIC (Fig. 4; Appendix S8: Tables S1–S2). This improvement was most pronounced relative to the mean environmental model and to a lesser extent when compared to the instantaneous acclimation model (Fig. 4).

Model performance also depended importantly on both the starting temperature and amplitude of fluctuations (Fig. 5). In constant environments, all three models agree; as amplitudes increase, model performance diverges. Averaging across initial temperatures, the gradual acclimation model has the lowest mean absolute error (MAE) when fluctuations $>3.5^{\circ}\text{C}$ in *C. reinhardtii*, and performs similarly to the instantaneous model in *M. aeruginosa* (averaged across initial temperatures; Fig. 5). Both models increasingly improve on the mean temperature model as amplitude rises (Fig. 5). However, there are important interactions between amplitude and starting temperature (Fig. 5; Appendix S5: Fig. S2). We can contextualize these by calculating how instantaneous and gradual acclimation model predictions diverge across a continuous range of treatments (Appendix S5: Fig. S3). This reveals regions where the models are expected to predict similar final densities (despite assuming different mechanisms), as well as large regions where they diverge; these largely align with experimental results (Appendix S5: Fig. S3). The emerging picture is one where gradual acclimation yields significantly different (and often better) predicted final densities at higher amplitudes ($>3.5^{\circ}\text{C}$) in *C. reinhardtii*, and that these effects are influenced by the starting temperature.

Similar patterns emerge in *M. aeruginosa*, albeit at higher amplitudes ($>5^{\circ}\text{C}$).

Extending this work to more complex patterns of environmental variation using our parameterized models, we find that thermal variation measured in Reed Lake, Portland, Oregon, USA, is sufficient to create situations where gradual acclimation can increase, decrease, or have limited influence on *C. reinhardtii* growth rates relative to instantaneous acclimation, in different time periods (Fig. 6; Appendix S6: Figs. S1–S3, DataS1: “Predictions for lake env.cdf”). Similarly, the environmental and ecological conditions jointly determine the extent to which in thermal acclimation alters growth in idealized sinusoidal environment (Appendix S7: Fig. S1, DataS2: “Predictions for sinusoidal env.cdf”).

DISCUSSION

We have presented a general framework, organized around the phenotype \times environment performance landscape (Chevin et al. 2010), that accounts for the ecological effects that accumulate during gradual plastic responses. We show empirically that gradual plasticity (in the form of thermal acclimation) meaningfully alters population dynamics over many domains of thermal variation and particularly for environments with larger fluctuations. Depending on the type of variation, these effects can increase, decrease, or have minimal effect on performance relative to acclimated expectations. By incorporating gradual plasticity into a predictive model, we are able to produce forecasts that qualitatively matched observed patterns of phytoplankton growth in

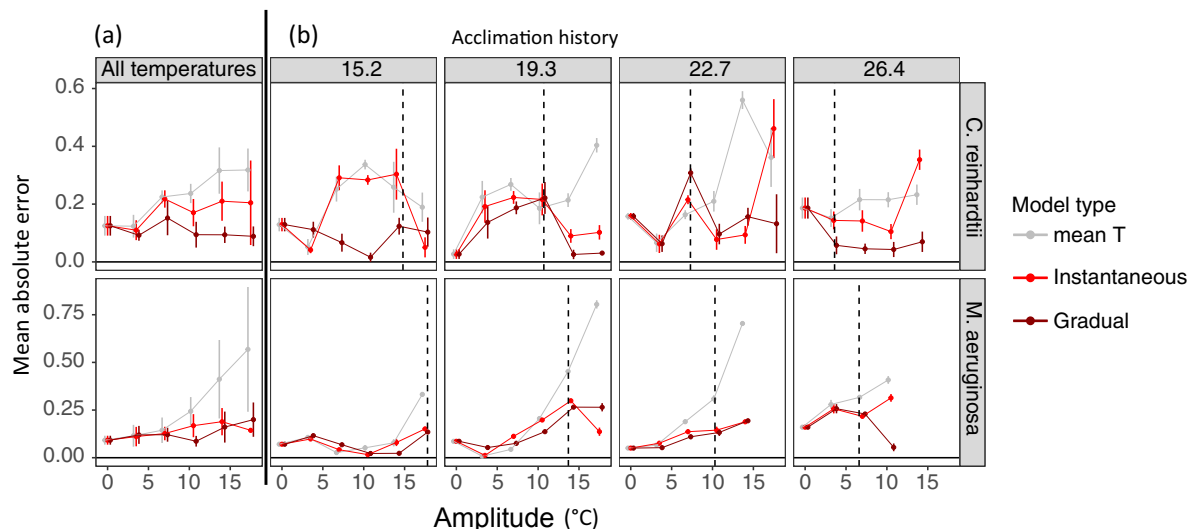


FIG. 5. Model performance varies with fluctuation amplitude and acclimation history. (a) Pooling populations with different acclimation temperatures, the mean absolute error (MAE) of the gradual acclimation model (dark red) remains low despite increasingly large fluctuation amplitudes (in degrees Celsius). At higher amplitudes, the mean T (gray) model performs poorly. Above $\sim 3.5^{\circ}\text{C}$ the instantaneous acclimation model (red) fares worse than the gradual acclimation model in *Chlamydomonas reinhardtii* (top row), but performs similarly on average in *Microcystis aeruginosa* (bottom row). (b) Interactions between acclimation history and fluctuation amplitude are also important, albeit complex due to nonlinearities (see also Appendix S5, Fig. S3). Data are means with $\pm 95\%$ confidence intervals. Vertical dashed lines indicate the species specific T_{opt} values for growth rate.

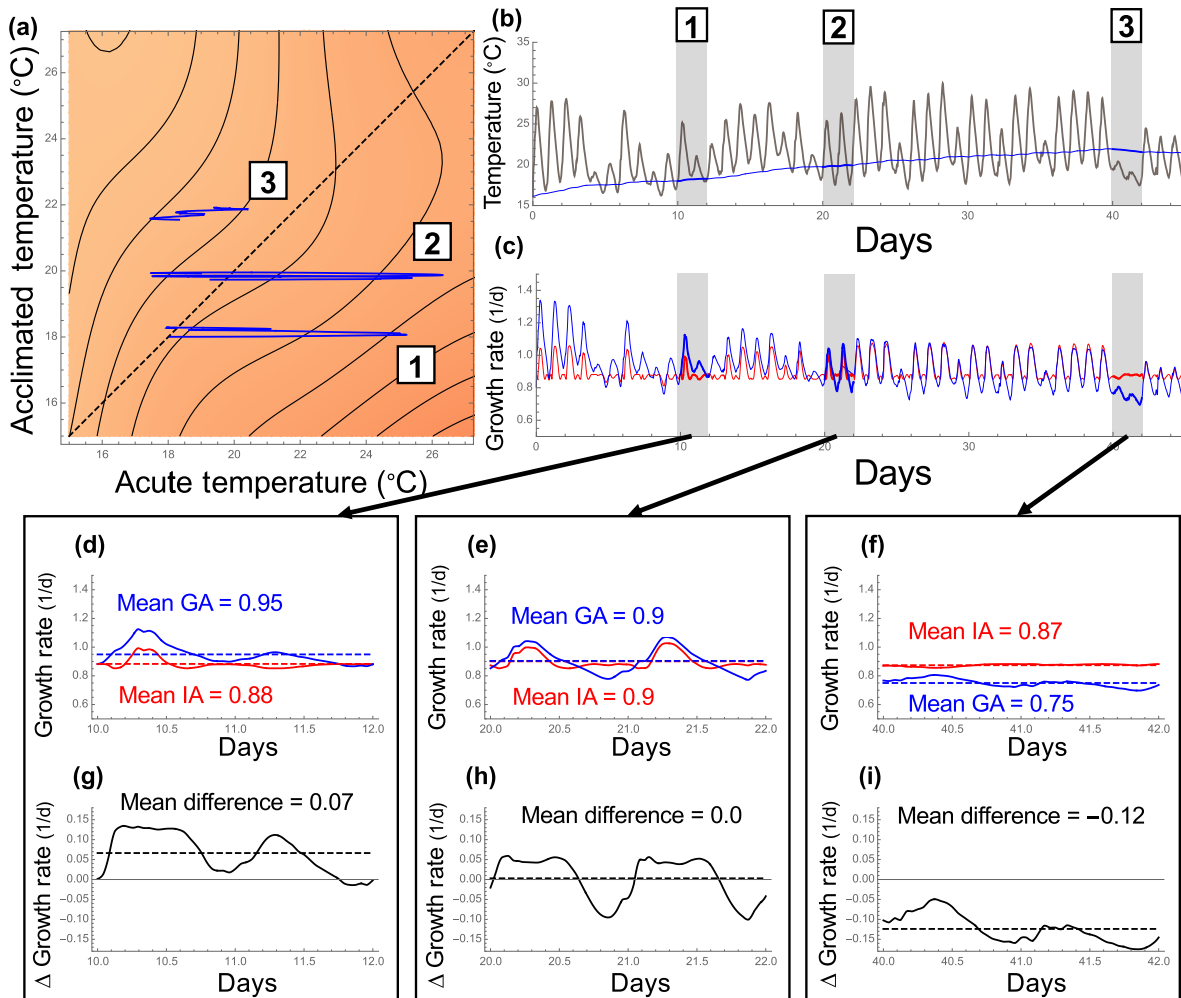


FIG. 6. A measured performance landscape (a), such as for *Chlamydomonas reinhardtii* (Fig. 2), can be combined with a 45-d temperature time series (b, gray line; from Reed Lake, Portland, Oregon, USA), and used to forecast population growth rates. Under instantaneous acclimation (IA, $\sigma = \infty$), a population's acclimation phenotype perfectly tracks these thermal dynamics. Gradual acclimation (GA, $\sigma = 0.0646$) dampens and delays the response of acclimation phenotype to temperature changes (b, blue line). Estimates of population growth rate dynamics over this time period (c) diverge between IA (red) and GA (blue) models. Focusing on illustrative 2 d windows reveals three scenarios (1–3, shaded boxes), corresponding to snapshots of each model's estimated growth rates (d)–(f) and their difference (g)–(i). In scenario 1, temporally averaged GA growth rates exceed IA growth rates (d) and (g), the two models agree on average in scenario 2 (e) and (h), and IA values exceed GA values in scenario 3 (f) and (i). Additional details and interactive examples appear in Appendix S6.

thermally variable environments, improving on models that neglect thermal acclimation. Given the ubiquity of environmental variation, resolving when and how gradual plasticity (such as thermal acclimation) operate may be key to understanding and predicting ecological dynamics.

Ecological and environmental contexts where thermal acclimation matters

Although we have considered thermal acclimation in a specific system, thermal acclimation is ecologically relevant in many contexts. We demonstrated that acclimation matters most in our system in regimes

with significant temporal variability, periodic high temperatures, and asymmetric patterns of temperature change. Such properties are reasonably common in aquatic ecosystems, where small (<3 km²) lakes, comprising the vast numeric majority of the world's lakes (Cael and Seekell 2016), exhibit average daily surface temperature fluctuations of 4–7°C (Woolway et al. 2016). Terrestrial ecosystems are generally more temporally variable than aquatic systems, experiencing a >5°C mean range of diurnal temperature fluctuations in tropical and temperate latitudes (Wang and Dillon 2014), which may be sufficient for gradual acclimation to have meaningful ecological consequences for terrestrial organisms.

Our data suggest that environments that are close to or exceed temperatures that correspond to maximum fitness (i.e., T_{opt}) create the conditions over which gradual plasticity can strongly influence an individual's performance, due to both the nonlinear and skewed nature of the acclimated performance curve and the potential for acclimation to alter the location of zero-net-growth isoclines (T_{min} and T_{max} ; Fig. 2). Because operative temperatures (i.e., the hypothetical body temperatures individuals achieve as a result of their physical properties and environment) routinely exceed both air temperatures and T_{opt} estimates (Sunday et al. 2016), instances where body temperatures exceed T_{opt} may be unexpectedly common, particularly for tropical terrestrial ectotherms where upper thermal limits (T_{max}) vary remarkably little relative to related taxa at other latitudes (Sunday et al. 2011). It appears that T_{max} values actually decline modestly in populations acclimated to hotter temperatures (especially in *M. aeruginosa*), suggesting that certain populations acclimated to extreme temperatures may be less tolerant of further warming. This result departs from the prevailing notion that thermal acclimation will provide a universally positive buffering capacity against physiologically stressful temperature regimes (Rohr et al. 2018). Such instances of detrimental acclimation (e.g., acclimating reducing the performance of organisms) may be highly important for estimating local extinctions expected under climate warming as growth rates shift between positive and negative values.

Additionally, because our measured performance landscapes are not symmetrical around the 1:1 line (Fig. 2, dashed line, where acclimated and acute temperatures are identical), perturbations starting from cold vs. hot conditions will not have comparable effects. In general, growth rate tended to exceed acclimated expectations when populations were previously cold acclimated, and fall short of acclimated expectations when populations were previously warm acclimated, particularly for *M. aeruginosa*. Thus, short-term asymmetries in patterns of experienced temperature, or situations with non-stationary environmental variation, may produce conditions where asymmetries of the performance landscape matter for the outcome of ecology (see Fig. 6 and Appendix S6: Figs. S1–S3 for effects in Reed Lake). For example, organisms that behaviorally thermoregulate during the day, but not at night, will start each day from a cold-acclimated state, and initially experience cold to hot perturbations (Logan et al. 2019). Indeed, many lines of research document that phenotypic and fitness responses to a particular environmental cue depend on the temporal patterning of the cue. For example, the temporal patterning of light flecks impacts CO_2 assimilation in understory plants (Chazdon 1988, Sims and Pearcy 1993), the temporal patterns in stimulus triggers behavioral habituation of defensive responses in plants (e.g., *Mimosa* [Gagliano et al. 2014]) and animals (e.g., sea anemones (Logan 1979), and temperature decreases induce a varied amount of cold-hardening responses in

insects (Overgaard et al. 2007). Such responses are highly suggestive of gradual plasticity operating at ecologically relevant timescales, because instantaneous acclimation is not capable of producing such time-dependent responses (as described in motivating Fig. 3).

Generalizing gradual plasticity beyond phytoplankton

The ecological impacts of gradual plasticity likely extend to other groups of organisms beyond phytoplankton. Phytoplankton have fast per capita exponential growth rate of $\sim 1/\text{d}$, similar rate to other unicellular prokaryotes and eukaryotes (Savage et al. 2004), and some small multicellular eukaryotes (Stemberger and Gilbert 1984). In this case, birth and death rates will unfold on similar timescales as the acclimation rates measured in our experiments, indicating that mismatches due to environmental variability at a daily timescale will produce effects that occur on a multigenerational timescale (Rescan et al. 2020). For such organisms, there exists a potential for convergence of gradual plasticity and rapid evolution. Although not explicitly explored, evolution was unlikely to exert much influence on this study, given initial bottlenecks, the low number of generations over which assays were conducted, and widespread observations of phenotype–environment mismatches that increased performance (Kremer et al. 2018).

For organisms with longer generation times, gradual plasticity could influence population dynamics by one of two processes. First, acclimation to abrupt environmental changes could unfold much more slowly than observed in our study, such that single perturbations could directly interact with demographic rates of longer-lived organisms. For example, physiological acclimation to abrupt novel temperature regimes in an experimental setting occurred over several years and across generations in the tropical damselfish *Acanthochromis polyacanthus* (Donelson et al. 2012) and across weeks to years within a generation in boreal tree species (Reich et al. 2016). Such a shift could also occur based on interactions between environmental conditions and demography or development. For example, the quality of habitats experienced by juveniles may produce carryover (e.g., silver spoon) effects, influencing the performance of subsequent life stages in different environments (Lindström 1999). Such effects may be operating in our experiments, where phytoplankton populations acclimated to cold environments were generally able to outperform populations acclimated to a range of warmer conditions even in warmer acute environments.

Secondly, it is possible that for longer-lived organisms, the cumulative impacts of short-lived phenotypic mismatches can impact demographic rates, even with acclimation rates comparable to those observed in our experiments. For example, Woods and Kingsolver (2016) predicted large cumulative differences in the biomass accumulation of *Manduca sexta* caterpillars based on whether individuals did or did not produce heat shock

proteins in response to diel temperature fluctuations. Here, the opportunity for daily phenotypic mismatch compound over time and such cumulative impacts on biomass would likely ultimately impact fitness (Kingsolver and Huey 2008). In such cases, any alterations to existing patterns of environment variability that may be coincident with climate warming, such as increased variability at sub-weekly timescales (Wang and Dillon 2014, Woolway et al. 2021) could alter ecology based on the consequences of gradual plasticity. Indeed, for the two phytoplankton species we explored, many higher amplitude environments produced instances of gradual acclimation reducing performance below instantaneous acclimation expectations (Appendix S5: Fig. S2). However, over short timescales, effective ecological prediction may simply require accounting for acute effects, and not the full complexity of gradual acclimation dynamics (e.g., the response to variation of the slower-acclimating *C. reinhardtii* is reasonably predicted by its acute response alone, given a known starting phenotype; Appendix S8, Tables S1 and S2).

The mechanisms underlying phenotypic change is another important consideration informing the existence and effects of gradual plasticity. The exact physiological mechanism(s) underpinning the responses we observe are presently unknown, although there are likely candidates. It is known that temperature affects stoichiometry. For example, phytoplankton generally have lower C:P and C:N ratios under colder conditions (marine: Toseland et al. [2013], Yvon-Durocher et al. [2015], in freshwater: Rhee and Gotham [1981], De Senerpont Domis et al. [2014]). As such, cells acclimated to colder temperatures store excess quantities of limiting nutrients (N and/or P) that are not required for growth, but may fuel future growth when conditions warm. Additionally, respiration and photosynthesis rates are strongly temperature-dependent processes (Anning et al. 2001, Padfield et al. 2016, Baker et al. 2016). For example, when exposed to low temperatures, the brown algae *Laminaria saccharina* immediately exhibits reduced light harvesting efficiency and increased respiration relative to cultures acclimated to higher temperatures (Davison 1991). Other processes allowing plasticity, such as the production of heat shock proteins in response to various environmental stressors, may be shared across taxa (Kingsolver and Woods 2016, Mühlhofer et al. 2019). Future research focusing on the mechanisms underlying gradual plasticity will be key for generalizing the response of organisms outside of *C. reinhardtii* and *M. aeruginosa*.

In summary, understanding and anticipating ecological responses to variable and novel environmental conditions requires both uncovering fundamental biological processes and integrating these mechanisms into ecological predictions (Doak et al. 2008, Singer et al. 2016, Pennekamp et al. 2019). We present a simple framework, the performance landscape, which links phenotype, environment, and performance, and makes it possible to consider the ecological impacts of gradual plasticity. We

demonstrate in multiple ways that omitting this dependence on historical conditions caused by gradual plasticity leads to inadequate predictions of algal population dynamics in a range of variable environments under laboratory conditions, and likely under real-world conditions. We argue that these responses are specific cases of a general and underappreciated phenomenon, gradual plasticity, which may affect a wide range of other organisms, performance metrics, environmental drivers, and ecological processes. Exploring how populations respond to multiple stimuli in nature through plastic and evolutionary mechanisms (Cortez 2011) that ultimately shape relationships between organisms and environments, represents a key avenue for improving our understanding of ecology in a variable world.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1478/full>

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Data (Fey et al. 2021) are available in the Dryad digital repository: <https://doi.org/10.5061/dryad.05qfttf2s>.