Introduction

Periods of extreme environmental warming are increasingly driving mass mortality in both aquatic and terrestrial ecosystems, altering the composition and diversity of ecological landscapes (Welbergen et al. 2008; Allen et al. 2010; McKechnie and Wolf 2010; Hughes et al. 2018b; Robinson et al. 2019). The frequency, intensity, and duration of periods of extreme warming are expected to rise over the next hundred years (Meehl and Tebaldi 2004; Rahmstorf and Coumou 2011; IPCC 2014) and play an increasing role in species loss resulting from climate change (Hoffmann et al. 2013; Kingsolver et al. 2013; Thompson et al. 2013; Vasseur et al. 2013; Williams et al. 2013; Urban 2015; McManus et al. 2020), and yet we know relatively little about the effects that recurring periods of extreme warming will have on variability in community composition (Ma et al. 2015; Buckley and Huey 2016b). This is because our understanding of the complex and interacting ecophysiological processes underpinning the relationship between climate and biodiversity is still developing (Sinclair et al. 2016; Sears et al. 2019).

With respect to the effects of extreme warming on community composition, research demonstrates that the ability of a species to survive extreme warming rises and falls with increasing temperature according to thermal performance curves, which can also be referred to as thermal reaction norms (Huey and Stevenson 1979; Huey and Kingsolver 1989; Angilletta 2009). Thermal performance curves show how functional traits contributing to a species’ fitness (e.g., locomotion [John-Alder et al. 1988], foraging activity [Cerdà et al. 1998], feeding rate [Rall et al. 2012], metabolism [Kellermann et al. 2019], and population growth rate [Lühring and DeLong 2017]) respond to changes in temperature, including indicating the optimal performance temperature (the temperature at which performance is maximized), thermal breadth (the range of temperatures across which the trait functions), and thermal limits (the temperatures resulting in death). Performance curves tend to be unimodal and roughly Gaussian in shape (Angilletta 2006), but the temperatures that correspond to optimal performance,
stressful conditions, and death can vary widely across species forming a community (Kordas et al. 2011). As a consequence, rising temperature during extreme warming can drive species-specific patterns of thermal stress (Laakso et al. 2003; Fey and Cottingham 2012) and potential changes in interspecific interactions (Jiang and Morin 2004; Luhring and DeLong 2016; Comeault and Matute 2021), resulting in deterministic patterns of community disassembly (i.e., nonrandom sequence of species loss due to environmental change; Zavaleta et al. 2009).

Research shows that the ability of species to survive extreme warming is also affected by warming rates (Mora and Maya 2006; Terblanche et al. 2007). However, the effect that different warming rates have on patterns of community disassembly is not well understood (Zavaleta et al. 2009; fig. 1). This knowledge is important for understanding the potential effects that increasingly frequent and destructive periods of extreme environmental warming may have on variability in community composition in disturbed environments. That knowledge can also help evaluate the

Figure 1: Two ecological scenarios illustrating the biological significance of changes in sequence of species loss during environmental warming. Temperature bars indicate survival of three species (A, B, and C) in a community during low and high rates of warming (e.g., in a, species A survives low and high rates of warming to maximum temperatures of 36°C and 38°C, respectively). a, Warming rate does not alter sequence of disassembly. Different communities of species survive when temperature rises at different rates to the same maximum temperature. However, because the warming rate does not alter the sequence of disassembly, no rate-specific communities exist (i.e., there is no difference between the sets of possible communities surviving low and high rates of warming). As a result, the set of possible surviving communities across both rates is limited to [A, B, C] or [B, C] or [C]. b, Warming rate alters sequence of disassembly. Like scenario a, different communities of species survive when temperature rises at different rates to the same maximum temperature. However, because the warming rate alters the sequence of community disassembly, rate-specific communities [B, C] and [A, C] are possible, increasing the total number of possible surviving communities across both rates from three to four: [A, B, C] or [B, C] or [A, C] or [C]. The greater the proportion of communities that are rate specific, the more important the role of the warming rate (per se) for the generation of differences in community composition.
extent to which warming rates might alter the relative risk and timing of loss of species from a community. In this study, we asked two questions: First, how variable is the sequence of disassembly resulting from environmental warming (in other words, to what extent is the sequence of species loss deterministic as opposed to random)? Second, can different warming rates alter the sequence of disassembly (fig. 1)? For the first question, we hypothesized that the sequence of disassembly would be more deterministic than random, reflecting the preponderance of research showing that the lethal effects of both biotic and abiotic environmental stressors on species survival are predictable and determined by fundamental ecological processes (Angilletta 2009; Morin 2011). Regarding the second question, studies show that the relationship between the warming rate and the temperature at which an individual species is lost can vary substantially. In some studies, the ability of a species to survive to higher temperatures has consistently increased with the warming rate, evidence of a positive relationship between the warming rate and the temperature of loss (Terblanche et al. 2007; Allen et al. 2016). In other studies, the ability to survive to higher temperatures has consistently decreased with the warming rate, evidence of a negative relationship between the warming rate and the temperature of loss (Chidawanyika and Terblanche 2011; Vinagre et al. 2015). A limited number of studies examining the effect of extreme ranges of warming rate (e.g., the slowest and fastest differing by several orders of magnitude) have documented mixed relationships, with the temperature of loss increasing, decreasing, or not changing depending on the range of rate examined (Elliott and Elliott 1995; Mora and Maya 2006). We hypothesized that similarly idiosyncratic relationships between the warming rate and the temperature of species loss might exist among species forming an ecological community and that if those relationships differed sufficiently, relative thermal tolerances of species would depend on warming rates (i.e., species A surviving to a higher temperature than species B at one rate but to a lower temperature than species B at another rate), in which case different warming rates would be expected to drive changes in the sequence of disassembly. The ecological mechanisms driving reversals in the relative thermal tolerances of species at different warming rates, which were not explored in this study, might be both abiotic (e.g., differences among species in their sensitivity to the intensity and duration of heat exposure [Terblanche et al. 2007; Rezende et al. 2014, 2020] and differential opportunities for thermal adaptation [Hao et al. 2015; Buckley and Huey 2016a; Grant et al. 2017; Nadeau et al. 2017]) and biotic (e.g., effects of different warming rates on temperature-dependent species interactions; Jiang and Morin 2004; Barton and Schmitz 2009; Gilbert et al. 2014), both considered in detail in “Discussion.”

Methods

Experimental System

We conducted our experiment using a community of four rotifers and six ciliates extracted from the eutrophic shallows of Bamboo Pond at Rutgers Gardens in 2012. Thereafter, the community was propagated in the lab through serial dilution in covered 1.0-L glass containers and under standardized culturing conditions (supplemental PDF, available online) roughly approximating its natural summertime environment. After extraction of organisms from the university pond, no species were added to the community, and all glass containers, lids, detritus, water, and instruments in contact with the community were sterilized before use. As a result, the final community included rotifers and ciliates feeding on a naturally occurring background assemblage of bacteria, algae, and fungi, all exhibiting coexistence under standard laboratory culturing conditions for more than 4 years before the start of this experiment. This ensured that the sequence of disassembly in response to warming was the result of experimental treatments rather than inherent instability in the community. Species monitored in the experiment included four rotifers (Cephalodella sp., Lecane sp., Lepadella sp., and Rotaria sp.) and six ciliates (Aspidisca sp., Coleps sp., Euplotes daidaleos, Frontonia elliptica, Paramecium bursaria, and Paramecium caudatum). Representing a guild of algavores and bacterivores, together they included all species visually identifiable using a stereoscopic microscope at \( \times25 \) power. Experimental replicates were created immediately preceding the start of each treatment using standardized procedures (supplemental PDF).

Experimental Design

Both during and for 4 years preceding the start of the experiment, the source community for all experimental replicates was held in a climate-controlled room with heating and cooling backup systems at 23.5°C±0.73°C (room temperature). Upon commencing warming treatments, which were controlled using water baths (Cole-Parmer StableTemp, model EW-14576-16), all communities were first held for 2 weeks at an acclimation temperature of 26.0°C. Following the acclimation period, temperature was increased at one of three incremental warming rates (hourly rate: 0.5°C h\(^{-1}\); daily rate: 0.5°C day\(^{-1}\); weekly rate: 0.5°C week\(^{-1}\); experimental design summarized in fig. S1; figs. S1–S5 are available online). Establishing a shared acclimation temperature before ramping followed the dynamic method of determining relative temperature tolerances (Terblanche et al. 2007; Kingsolver and Umbanhowar 2018). We selected an acclimation temperature that was slightly higher than peak recorded room temperature (25.4°C), and both room temperature and acclimation temperature were within the range.
of measured water temperature on the day the community was extracted from the shallows of Bamboo Pond (see species densities at room and acclimation temperature in fig. S2). Bath temperatures were calibrated and monitored using dual digital thermometers, and water pumps circulated bathwater to reduce within-bath variation in temperature. Six replicates of the community held at room temperature as controls for the lethal effect of rising temperature were compared with hourly, daily, and weekly rate treatments.

Because of constraints of time and space, we conducted hourly, daily, and weekly rate treatments in month 1, month 2, and months 3–10 of the 11-month experimental term, respectively. The hourly and weekly rate treatments (n = 12 each) formed the core of the experiment, providing the primary data used to answer our study questions. We added the daily rate treatment (n = 6, replication constrained by remaining time and space) to provide supplemental data for an intermediate rate of warming. After completing hourly, daily, and weekly rate treatments, we repeated the hourly rate treatment in month 11 (n = 12, resulting in 24 total replicates for the hourly rate treatment) to allow analysis of the effect of differences in time resulting from staggering treatments. The first and last replicates of the hourly rate treatment, conducted at the beginning and end of the experimental term, respectively, had the most and least amount of time, respectively, of all 42 replicates in our experimental design. This allowed us to (a) test the effect of differences in time on the temperature of species loss in hourly rate replicates and (b) analyze whether significant patterns in the temperature and sequence of species loss observed across all replicates of all treatments correlated with the warming rate or the staggered timing of treatments.

Warming rates examined in this study were selected to roughly approximate the wide range of warming rates during and preceding periods of extreme temperature variously referred to as extreme high-temperature events, heat waves, extreme summers, the El Niño–Southern Oscillation (ENSO), the Southern Annular Mode, and other extreme recurring interannual climate events. Warming rates are determined by both stochastic (Berner et al. 2017) and recurring patterns of temperature volatility that can occur over the course of hours (Braganza et al. 2004), days (Whitman et al. 1997; Sardon 2007), weeks (Pfautsch and Adams 2013), and months (Wernberg et al. 2012; Kahn 2015). They also tend to be negatively correlated with the duration of the warming period. Warming periods associated with diurnal temperature cycles occur over the course of a single day, are generally presented in time-temperature series using either mean hourly temperature or minimum and maximum daily temperatures as data (Braganza et al. 2004), and are characterized by rates of warming that are among the highest observed in natural systems (exceeding fire and geothermal heating). In contrast, warming periods associated with modes of interannual climate variability (e.g., ENSO) occur over the course of many months, are generally presented in time-temperature series using mean weekly temperature as data (Wernberg et al. 2012; Kahn 2015), and are characterized by warming rates that are several orders of magnitude slower than those associated with diurnal temperature cycles (although considerably more rapid than warming rates associated with global warming). We restricted the scope of our study to examining the effect of warming rates because examining the combined effect of warming followed by cooling would have confounded the effects of warming and cooling rates on both sensitivity to temperature and patterns of species loss, effects that may be different.

### Data Collection

Immediately before each 0.5°C increase in temperature, we sampled replicate communities and identified all surviving species following standardized procedures (supplemental PDF). The sampling temperature at which no further organisms of a given species were observed alive (motile) represented the temperature of loss for that species and replicate. Recording the identity of all surviving species at each incremental change in temperature allowed us to both observe the sequence of species loss from the community (i.e., the sequence of disassembly) and generate a corresponding table of the distinct communities surviving at each temperature. Knowledge of the complete sequence of disassembly and corresponding temperatures of species loss provided information regarding the potential survivors of warming across a wide range of possible maximum temperatures (i.e., communities observed at lower and higher temperatures representing potential survivors of less and more extreme warming, respectively).

To test the effects of the warming rate on the sequence of disassembly, we analyzed the sequence (order) of species loss of the 10 species in each replicate. An order of 1 was assigned to the first species lost, 2 was assigned to the second, 3 was assigned to the third, and so on. Species lost at the same temperature shared the same order, which was the average of their respective orders had they been distinct (e.g., species a, b, c, and d lost at 32°C, 33°C, 33°C, and 34°C, respectively, would be assigned the orders 1, 2.5, 2.5, and 4, respectively).

To assess the contribution of the warming rate to variability in community composition, we compared all of the distinct communities of surviving species that were observed in hourly, daily, and weekly rate treatments throughout the period of ramping temperature. The percentage of all distinct communities that were rate specific (observed in at least one but not all rate treatments) provided a
quantitative measure of the contribution of the warming rate (per se) to variability in community composition (fig. 1).

All lights, water baths, timers, and pumps were attached to a 10-kVA online, double-conversion power supply (Tripp Lite, model SU10000RT3U2TF), which did not record any electrical faults during the experiment (for photos of the setup, see fig. S3).

**Statistical Analysis**

All statistical analyses were conducted in R (ver. 3.6.0; R Development Core Team 2019). We investigated consistency (randomness) in the sequence of species loss among the replicates of each rate treatment using Kendall’s coefficient of concordance. This provided a measure of the degree to which sequences of disassembly within each rate treatment were deterministic. We investigated whether the warming rate affected the sequence of loss of each species using the Kruskal-Wallis rank sum test, and *P* values were adjusted for multiple comparisons using the Benjamini-Hochberg method (Benjamini and Hochberg 1995). To consider how representative the range of communities observed in our experimental replicates was of all possible variability in community composition (i.e., the sum total of variability that we might expect would be possible given the means and variances in temperature of species loss observed in our experimental results), we ran a Monte Carlo analysis that simulated 10,000 additional replicates of both the hourly and weekly rate treatments. The Monte Carlo analysis allowed us to consider whether our estimate of the percentage of distinct communities that were rate specific (i.e., our quantitative measure of the contribution of the warming rate to variability in community composition) might materially change with increased replication. Each replicate was simulated by calculating a temperature of loss for each species, assuming that temperature would follow a standard normal distribution described by the mean temperature of loss and standard deviation observed in our experimental results. There were 24, 6, and 12 experimental replicates for the hourly, daily, and weekly warming rates, respectively. Hence, there were 24, 6, and 12 experimental observations of the temperature of loss of each species under the hourly, daily, and weekly warming rates, respectively. After computing the mean and standard deviation in temperature of loss by species and rate, we performed 10,000 Monte Carlo simulations; on each iteration, we generated a simulated temperature of loss from a normal distribution with a mean and standard deviation equal to the observed values for each species. These were then ranked, from lowest to highest temperature, simulating 10,000 additional replicates of the sequence of disassembly under each of the warming rate treatments.

To investigate the effect of time staggering treatments, we analyzed differences in the temperature of species loss in the two sets of replicates of the hourly rate treatment using the Wilcoxon-Mann-Whitney test (because data were in discrete 0.5°C increments). We analyzed similarity in the sequence of species loss among first and last replicates of the hourly rate treatment using Kendall’s coefficient of concordance. We analyzed correlation between our experimental results (both temperature and sequence of species loss) and possible sources of those differences (both differences in warming rates and timing of staggered treatments) using Spearman’s rank correlation coefficient. Time was equal to the number of months from the start of the experiment to the completion of each time-staggered replicate. All *P* values were adjusted for the effects of multiple comparisons (Benjamini and Hochberg 1995).

**Results**

During the treatment with the rate of 0.5°C h⁻¹, the 10 monitored species were lost from the community over the course of 24–44 h. During the treatments with rates of 0.5°C day⁻¹ and 0.5°C week⁻¹, the 10 species were lost from the community over the course of 12–36 days and 1–6 months, respectively. All 10 species were lost at lower temperatures in the weekly rate treatment than they were in the daily rate treatment and at lower temperatures in the daily rate treatment than in the hourly rate treatment (Wilcoxon-Mann-Whitney: all *P* < .001; fig. 2). Within each rate treatment (i.e., among the replicates of a single warming rate treatment), consistency in the sequence of species loss was very high (Kendall’s *W*: 0.5°C h⁻¹: *W* = 0.988, *χ²* = 213, *P* < .01; 0.5°C day⁻¹: *W* = 0.989, *χ²* = 53.4, *P* < .001; 0.5°C week⁻¹: *W* = 0.959, *χ²* = 104, *P* < .001).

Regarding the effect of warming rates on sequence of disassembly, across rate treatments, the warming rate affected the sequence of species loss for nine of 10 species (table S1; tables S1, S2 are available online). Differences in sequence of species loss were largely attributable to changes in the relative order of loss of three species (fig. 3). Throughout the experiment, all 10 species in the six control replicates held at room temperature coexisted without local extinctions, continuing the long-term (>4 year) pattern of coexistence preceding the experiment and indicating that the sequence of species loss observed in warmed communities was attributable to warming.

With respect to the effects of the warming rate on variability in community composition, we observed 22 distinct communities in the hourly, daily, and weekly rate treatments (figs. 4, 5, S4, S5a, S5b). A total of 77% of the communities were observed in at least one (but not all three)
rate treatments, presenting strong evidence for rate-specific communities. Distinct combinations differed by one or two species, representing 12%–50% of species present in the community. The Monte Carlo analyses (table 1; fig. S6) suggested that 42 additional distinct communities might be possible given the means and variances of temperature of species loss observed in our experimental results (note that if the sequence of species loss were random, 1,022 distinct

Figure 2: Mean number of surviving species and standard deviation for hourly rate \((n = 24)\), daily rate \((n = 6)\), and weekly rate \((n = 12)\) replicates at each 0.5°C incremental increase in temperature. Each of the 10 species was lost at lower temperatures in the weekly rate treatment than in the daily rate treatment and at lower temperatures in the daily rate treatment than in the hourly rate treatment (Wilcoxon-Mann-Whitney: all \(P < .001\)). Across species, temperature of loss fell 6°C–9°C when the warming rate was reduced from 0.5°C hr⁻¹ to 0.5°C week⁻¹.

Figure 3: Mean sequence of species loss and standard deviation in hourly rate \((n = 24)\), daily rate \((n = 6)\), and weekly rate \((n = 12)\) replicates. Across treatments, sequence of species loss differed significantly for all species but Euplotes sp. (table S1). Parallel and intersecting lines indicate consistency and reversals in relative sequence of loss, respectively. Asterisks indicate rotifers.
communities would be possible). Approximately 72% of all distinct communities identified in the Monte Carlo analysis were rate specific, consistent with our experimental results and demonstrating the importance of the warming rate for the generation of differences in community composition. Distinct combinations differed by one, two, or three species, representing 12%–50% of species present in the community.

Regarding our analysis of the effect of time staggering treatments, both temperature and sequence of species loss correlated very strongly with the warming rate but not with differences in time (tables S2a, S2b). Differences in
time among the first and last 12 replicates of the hourly rate treatment resulted in slightly lower (≤0.5°C) temperature of species loss for five of 10 monitored species (table S2c), but this had little effect on the overall pattern of species loss observed across all 24 replicates of the hourly rate treatment (Kendall’s coefficient of concordance [W] for all 24 hourly rate replicates was very close to 1.0; W = 0.988, χ² = 213, P < .0001). If time were driving trends in the sequence of species loss observed across rate treatments in this experiment, the sequences of species loss in the two sets of hourly rate replicates would have differed from each other far more than they differed from the replicates of the daily and weekly rate treatments (notice mean and SD in sequence of species loss; fig. 3). These findings support the conclusion that the significant trends in both temperature and sequence of species loss observed in this experiment were attributable to differences in warming rates rather than the staggered timing of treatments.

Discussion

This study provides experimental evidence that the sequence of species loss during periods of extreme warming can depend on the environmental warming rate and that changes in the sequence of species loss driven by the warming rate can play an important role in the generation of differences in community composition. With respect to effects of climate change, the results raise the possibility that differences in warming rates across space and time could eventually increase variability in community composition in environments disturbed by extreme temperature. An extensive literature shows that differences in community composition can have important long-term consequences for ecosystem function (Hooper et al. 2005), particularly when differences between communities are characterized by the presence or absence of species maintaining important ecosystem attributes (Petchey and Gaston 2006). Because functional traits of species differ greatly and regulate many ecosystem characteristics, increasingly variable community composition could result in altered interspecific interactions (Estes et al. 1998; Petchey et al. 2008; Zipkin et al. 2020), changes to the ecological environment potentially detrimental to species persistence (e.g., microsite variability in light, water, temperature, oxygen, and CO₂; Jones et al. 1994; Wright et al. 2002; Hom and Murray 2014), and modified rates of productivity and nutrient retention (Fukami...
and Morin 2003; Wagg et al. 2014). More variable community composition might also decrease the predictability of ecosystem attributes (e.g., ecosystem respiration) at finer scales of ecological organization (McGrady-Steed et al. 1997). Conversely, increased variability could also contribute to improved ecosystem function if species migration patterns and recolonization dynamics in disturbed landscapes are consistent with the spatial insurance hypothesis (Loreau et al. 2003; Wang and Loreau 2014; Limberger et al. 2019). The spatial insurance hypothesis describes an ecological scenario where dispersal among ecosystems in a spatially and temporally variable landscape allows for the coexistence of functionally complementary species. Over time, the coexistence of functionally complementary species maximizes mean ecosystem productivity and minimizes its variability, resulting in increased stability.

Across all 10 species, temperature of loss decreased by 6°C–9°C when the warming rate was lowered from 0.5°C·h⁻¹ to 0.5°C·week⁻¹, a finding consistent with studies demonstrating that temperature of species loss is positively correlated with the warming rate (Terblanche et al. 2007; Allen et al. 2016; Rezende et al. 2020). Positive correlation between the warming rate and the temperature of loss can be attributed to a fundamental ecophysiological relationship known for nearly a century: the higher the temperature, the shorter the period of time that an organism can tolerate it (Bigelow 1921; Maynard-Smith 1957; Cerdà and Retana 2000; Terblanche et al. 2007). This relationship is presented in empirically derived thermal death time (TDT) curves, which are isolines indicating combinations of constant temperature and exposure time resulting in the same probability of survival and which can be described mathematically as

\[
\log_{10} t = \frac{(T_{\text{max}} - T)}{z},
\]

where \(t\) is exposure time, \(T\) is exposure temperature (°C), \(T_{\text{max}}\) is the maximum temperature the species can survive for 1 min, and \(z\) is the species’ constant of thermal susceptibility, which characterizes how thermal tolerance decays with the duration of exposure (i.e., the reduction in constant exposure temperature \(T\) required to compensate for a 10-fold increase in exposure time \(t\); Rezende et al. 2014). The relationship presented in TDT curves is central to the concept of a species’ thermal tolerance landscape, a model created by superimposing TDT curves describing different survival probability isolines and that relates how the probability of surviving a constant temperature declines with both the exposure temperature and time (Rezende et al. 2014). Only recently, the thermal tolerance landscape was expanded into an even larger theoretical framework that could be used to predict the probability of surviving variable temperature conditions (e.g., rising temperature) using survival data from constant-temperature assays (Rezende et al. 2020). This framework predicts that, all else equal, a lower rate of warming should result in a lower temperature of loss, consistent with observations for all 10 species in this study. The underlying and mutually supporting premises of the theoretical framework are that (a) a lower warming rate increases exposure time at each temperature, (b) greater exposure time at each temperature increases cumulative thermal stress at each temperature, and (c) increased cumulative stress at each temperature results in a lower temperature of loss. While this study documents positive correlation between the warming rate and the temperature of loss, negative correlation has been observed in other species and attributed to beneficial thermal acclimation (Mora and Maya 2006; Chidawanyika and Terblanche 2011; Vinagre et al. 2015). Opposing detrimental effects of increased exposure time and beneficial thermal acclimation (often referred to as “hardening”) could be occurring simultaneously, in which case the sign of correlation observed across species and different ranges of warming rate may be determined by the relative strengths of the two effects (Terblanche et al. 2007). The potential effects of exposure time (both positive and negative) on performance and thermal limits under variable temperature conditions represent one of several possible ecological mechanisms accounting for changes in sequence of community disassembly at different rates of warming (discussed below) and can be conceptualized using hypothetical performance data for static and dynamic temperature assays (i.e., performance measured following different combinations of start temperature, end temperature, and rates of warming and cooling; fig. 6a).

### Table 1: Distinct communities observed in hourly, daily, and weekly rate treatments

|                | Experiment | Monte Carlo analysis |
|----------------|------------|----------------------|
| Shared         | 5          | 18                   |
| Rate specific  | 17         | 46                   |
| Total          | 22         | 64                   |
| Rate specific (%) | 77       | 72                   |

Note: Experimental and Monte Carlo analysis results are presented side by side for comparison and summarize details provided in figures 4 and S6. Shared communities were observed in all three rate treatments. Rate-specific communities were observed in at least one but not all three rate treatments. The percentage of distinct communities that are rate specific represents a measure of the contribution of the warming rate to variability in community composition. In the Monte Carlo analysis, distinct combinations differed by one, two, or three species, representing 15–66% of species present in the community. Both the experimental and Monte Carlo analysis results suggest that a substantial proportion of variability in sequence of disassembly and resulting community composition is driven by the warming rate.
Figure 6: a, Hypothesized effects of exposure time on performance and thermal limits under variable temperature conditions. Variable-temperature curves indicate species performance after being warmed/cooled from a constant start temperature ($T_{\text{start}}$) to the abscissa temperature ($T_{\text{end}}$) at a low rate (dark gray), medium rate (medium gray), and high rate (light gray). In this presentation, $T_{\text{start}}$ is equal to the optimal performance temperature ($T_{\text{opt}}$). The constant-temperature curve (black) indicates species performance at a constant $T_{\text{end}}$ (measured after held at that temperature for a period of time sufficient to allow performance to stabilize). By definition, all variable-temperature curves intersect the constant-temperature curve where $T_{\text{start}} = T_{\text{end}}$, and sections of variable-temperature curves corresponding to $T_{\text{end}}$ lower and higher than $T_{\text{start}}$ represent cooling and warming scenarios, respectively. Effects of cooling and warming rates on temperature of species loss ($R_c$ and $R_w$, respectively) equal the difference between the temperature of loss in constant- and variable-temperature curves. In this scenario, temperature of loss is positively and negatively correlated with warming and cooling rates (respectively) to be consistent with the Rezende et al. (2014, 2020) theoretical frameworks and the warming results of this study, although effects of beneficial thermal acclimation and evolution are also possible. To present the effects that differences in $T_{\text{start}}$ have on performance and thermal limits, a third variable (Z-axis) for $T_{\text{start}}$ could be included, in which case the point at which all variable-temperature curves intersect in three-dimensional space shifts along the constant-temperature curve with changes in $T_{\text{start}}$, and $R_c$ and $R_w$ approach zero as $T_{\text{start}}$ converges on cold and warm temperature of loss, respectively. b, Hypothetical variable-temperature performance curves (low-rate warming, dark gray; high-rate warming, light gray) for two species (1, solid line; 2, dashed line) presenting an ecological scenario where temperature of loss is positively correlated with the warming rate, and high- and low-warming rates result in altered sequence of species loss (high-rate temperature of loss [$H$]; low-rate temperature of loss [$L$]). Species 1 has the highest temperature of loss out of all scenarios ($H_1$) but also the largest effect of the warming rate on temperature of loss ($R_{w(1)}$). Theoretical frameworks for predicting temperature tolerance suggest that this scenario could occur if the temperature tolerance of species 1 is more sensitive to exposure time (i.e., the duration of warming) and the temperature tolerance of species 2 is more sensitive to exposure temperature (i.e., the intensity of warming; Rezende et al. 2014, 2020).
Highly consistent sequences of disassembly observed in this study suggest that deterministic processes may play a more important role than random processes in determining sequence of species loss. Across the 10,000 simulated replicates of the hourly and weekly rate treatments, only 156 and 87 distinct sequences were recorded, respectively, of them representing rare ecological outcomes (see fig. S6). Were the sequence of disassembly random, approximately 3.2 million distinct sequences would have been possible, each having the same expected probability. Ecophysiological processes leading to highly deterministic patterns of species loss during extreme heating, which were not explored in this study, may have varied by species and rate and could have included the effects of high temperature on the function of cellular enzymes (Hochachka and Somero 2002; Somero 2020), on the conformation of cellular membranes (Hazel and Williams 1990; Hazel 1995), on the ability of species to maintain aerobic metabolism (Pörtner 2001; Schulte et al. 2011; Pörtner et al. 2017), and on direct and indirect forms of interspecific interaction affecting species survival (Jiang and Morin 2004; Gilbert et al. 2014; Hughes et al. 2017).

In this study, differences in the sequence of species loss were mostly attributable to the effects of rate on three species (Rotaria sp., Cephalodella sp., and Paramecium bursaria). The remaining seven species largely retained their mean relative positions within the overall sequence of species loss across the three warming rates. It might be inferred from this information that these seven species share remarkably similar rate-response functions (i.e., the function describing the effect of warming rate on temperature of loss), perhaps because they face similar ecological stresses and/or employ similar short-term survival mechanisms with similar efficacy across warming rates. Importantly, this study examined the effect of rate on a small community of species with similar size, behavior, habitat, and ecological role, all factors that may shape rate-response functions. The effect of different warming rates in larger ecosystems, where diversity is orders of magnitude greater and variation in size, behavior, habitat, and ecological role of community members is far more extreme, may be substantially larger.

Several ecological mechanisms may be responsible, singly or together, for changes in sequence of disassembly at different rates of warming. First, species may differ in their fundamental physiological abilities to tolerate warming periods of varying intensity and duration. Conceptualized within the context of the TDT curve and the Rezende et al. (2014, 2020) theoretical frameworks, changes in sequence of species loss could occur at different rates of warming if one species in the community has both a higher $T_{\text{max}}$ and $z$ (the maximum temperature the species can survive for 1 min and its constant of thermal susceptibility, respectively) and another species in the community has both a lower $T_{\text{max}}$ and $z$. These circumstances may be common, as some analyses show that the parameters of $T_{\text{max}}$ and $z$ are highly positively correlated across species (variation in $z$ accounting for 85% of the variation in $T_{\text{max}}$), potentially indicating that evolution of temperature tolerance involves trade-offs with respect to the intensity and duration of the heat exposure (Rezende et al. 2014; but see Jørgensen et al. 2019). Species with high $T_{\text{max}}$ and $z$ can tolerate extreme temperatures for short periods of time, but their temperature tolerance drops rapidly as exposure time increases (i.e., their ability to survive is more sensitive to exposure time than to exposure temperature). Species with low $T_{\text{max}}$ and $z$ can tolerate moderately stressful temperatures for long periods of time, but reductions in exposure time result in only minor improvements in temperature tolerance (i.e., their ability to survive is more sensitive to exposure temperature than to exposure time). Following the Rezende et al. (2020) framework, if the differences in the parameters of $T_{\text{max}}$ and $z$ are sufficient to cause the TDT curves (and therefore also thermal tolerance landscapes) of the two species to intersect, the species with the higher $T_{\text{max}}$ would have the higher temperature of loss when warming rates are high (i.e., when exposure time is short), and the species with the lower $z$ would have the higher temperature of loss when warming rates are low (i.e., when exposure time is long; fig. 6b). Second, changes in sequence of disassembly may be driven by effects of the warming rate on temperature-dependent interspecific interactions. Many interspecific interactions affecting species survival are sensitive to changes in temperature (Tylianakis et al. 2008), including competition (Jiang and Morin 2004; Urban et al. 2012; Alexander and Levine 2015; Comeault and Matute 2021), predation (Barton and Schmitz 2009; Gilbert et al. 2014; Luhring and DeLong. 2016; Daugaard et al. 2019), and mutualisms (Warner et al. 1999; Pandolfi 2011; Hughes et al. 2017). During periods of extreme warming, interactions that are sustainable at lower temperatures may become unsustainable at higher temperatures, accelerating population decline and extinction by interacting with temperature to reduce demographic growth rates (i.e., driving additional population decline through more traditional effects of competition and predation on life history parameters affecting population size). However, slow warming may allow more time for the outcomes of altered interactions to play out than rapid warming, and so the effects of interspecific interactions on sequence of loss may be rate dependent (i.e., more likely to occur during slow warming than rapid warming). If so, rapid warming may generate outcomes determined primarily by differences in species’ fundamental physiological tolerances, while slow warming allows changes in species interactions to play out, a difference that could potentially result in altered sequence of disassembly. Third, differences in sequence of disassembly might be driven by differences...
in opportunities for adaptation. Adaptation to extreme salinity (Bell and Gonzalez 2011) and temperature (Lindsey et al. 2013) has been shown to be more likely during low rates of change than during high rates of change, and some species adapt to change more quickly than others, depending on their population size, generation time, method of reproduction, available genetic diversity, and other factors (Hoffmann and Sgró 2011; Carlson et al. 2014; Buckley and Huey 2016). This raises the possibility that rapid warming may generate outcomes determined primarily by pre-existing thermal tolerances, while slow warming generates outcomes influenced more by opportunities for evolution that differ among species and therefore have the potential to alter sequence of disassembly. In summary, if the combined effect of the mechanisms described above on temperature of loss varies with the warming rate differentially across species, then the sequence of disassembly may depend on warming rates. The higher the species richness of an ecosystem and the greater the effect of different warming rates on sequence of disassembly, the greater the possible variability in community composition and the larger the percentage of those combinations that will be rate specific (i.e., the more significant the potential role of the warming rate in the generation of differences in community composition). Importantly, effects of warming rates will be highest where species share similar upper thermal limits and future periods of extreme warming exceed those limits, as might occur in tropical communities of ectotherms (e.g., corals [Hughes et al. 2018a], lizards [Huey et al. 2009], amphibians [Sunday et al. 2014], and insects [Deutsch et al. 2008]).

Periods of extreme environmental warming will continue to be driven by both stochastic (Berner et al. 2017) and recurring (Braganza and Arblaster 2004; Arblaster and Alexander 2012) patterns of temperature variability. Researchers are increasingly speculating that the effects of global warming on oceanic and atmospheric circulation patterns (Petoukhov et al. 2013; Counou et al. 2015; Horton et al. 2015) may alter future temperature variability on regional scales (Huntingford et al. 2013; Screen 2014; Rehfeldt et al. 2018). If so, changes in the amplitude and persistence of extreme temperature anomalies, both increases and decreases, may alter intrinsic rates of warming, which the results of this study suggest could have potential consequences for future community composition.

Acknowledgments

We are grateful to Peter Morin and Henry John-Alder for lab space, access to supplies and equipment, technical assistance, and many fruitful discussions that greatly improved this study. We thank Julie Lockwood, Lin Jiang, Tim Casey, and members of the Morin Lab for comments on experimental design and the manuscript and Anthony Broccoli for helpful discussion of characteristics of temperature volatility in natural systems. We thank Jonathan Garbolino and Clint Burger for help designing, building, and maintaining critical power infrastructure and Kenneth Elgersma for his review of R code. We also thank Editor Jennifer Lau, Associate Editor Jeremy Fox, and two anonymous reviewers for many insightful comments that greatly improved the manuscript. P.B.W. was supported by an Albert Fellows Fellowship from the Rutgers School of Environmental and Biological Sciences.

Statement of Authorship

P.B.W. and E.J.G. designed the study; P.B.W. performed microcosm research, conducted related analyses, and provided funding for equipment; E.J.G. performed the Monte Carlo analysis; P.B.W. wrote the first draft of the manuscript; and both authors contributed substantially to revisions.

Data and Code Availability

All data files and R code for the Monte Carlo analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.qiq2vqgg; Walberg and Green 2021).

Literature Cited
Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species’ responses to climate change. Nature 525:515–518.
Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.
Allen, J. L., S. L. Chown, C. Janion-Scheepers, and S. Clussella-Trullas. 2016. Interactions between rates of temperature change and acclimation affect latitudinal patterns of warming tolerance. Conservation Physiology 4:cov053.
Angilletta, M. J. 2006. Estimating and comparing thermal performance curves. Journal of Thermal Biology 31:541–545.
———. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York.
Arblaster, J. M., and L. V. Alexander. 2012. The impact of the El Niño–Southern Oscillation on maximum temperature extremes. Geophysical Research Letters 39:2012GL053409.
Barton, B. T., and O. J. Schmitz. 2009. Experimental warming transforms multiple predator effects in a grassland food web. Ecology Letters 12:1317–1325.
Bell, G., and A. Gonzalez. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. Science 332:1327–1330.
Benjamini, Y., and B. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B 57:289–300.

Berner, J., U. Achatz, L. Batté, L. Bengtsson, A. De La Cámara, H. M. Christensen, M. Colangelli, et al. 2017. Stochastic parameterization toward a new view of weather and climate models. Bulletin of the American Meteorological Society 98:565–587.

Bigelow, W. D. 1921. The logarithmic nature of thermal death time curves. Journal of Infectious Diseases 29:528–536.

Braganza, K., D. J. Karoly, and J. M. Arblaster. 2004. Diurnal temperature range as an index of global climate change during the twentieth century. Geophysical Research Letters 31:L13217.

Buckley, L. B., and R. B. Huey. 2016. How extreme temperatures impact organisms and the evolution of their thermal tolerance. Integrative and Comparative Biology 56:98–109.

Carlson, S. M., C. J. Cunningham, and P. A. Westley. 2014. Ecosystem rescue in a changing world. Trends in Ecology and Evolution 29:521–530.

Cerdá, X., and J. Retana. 2000. Alternative strategies by thermophilic ants to cope with extreme heat: individual versus colony level traits. Oikos 89:155–163.

Cerdá, X., J. Retana, and S. Cros. 1998. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12:45–55.

Chidawanyika, F., and J. S. Terblanche. 2011. Rapid thermal responses and thermal tolerance in adult coding moth Cydia pomonella (Lepidoptera: Tortricidae). Journal of Insect Physiology 57:108–117.

Comeault, A. A., and D. R. Matute. 2021. Temperature-dependent competitive outcomes between the fruit flies Drosophila santomea and Drosophila yakuba. American Naturalist 197:312–323.

Coumou, D., J. Lehmann, and J. Beckmann. 2015. The weakening summer circulation in the Northern Hemisphere mid-latitudes. Science 348:323–327.

Daugaard, U., O. L. Petchey, and F. Pennekamp. 2019. Warming can destabilize predator-prey interactions by shifting the functional response from type III to type II. Journal of Animal Ecology 88:1575–1586.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghilambor, P. R. Martin, and D. C Haak. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the USA 105:6668–6672.

Elliott, J. M., and J. A. Elliott. 1995. The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. Journal of Fish Biology 47:917–919.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

Fey, S. B., and K. L. Cottingham. 2012. Thermal sensitivity predicts the establishment success of nonnative species in a mesocosm warming experiment. Ecology 93:2313–2320.

Fukami, T., and P. J. Morin. 2003. Productivity-biodiversity relationships depend on the history of community assembly. Nature 424:423–426.

Gilbert, B., T. D. Tunney, K. S. McCann, J. P. DeLong, D. A. Vasseur, V. Savage, et al. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology Letters 17:902–914.

Grant, P. R., B. R. Grant, R. B. Huey, M. T. Johnson, A. H. Knoll, and J. Schmitt. 2017. Evolution caused by extreme events. Philosophical Transactions of the Royal Society B 372:20160146.

Hao, Y. Q., M. A. Brockhurst, O. L. Petchey, and Q. G. Zhang. 2015. Evolutionary rescue can be impeded by temporary environmental amelioration. Ecology Letters 18:892–898.

Hazel, J. R. 1995. Thermal adaptation in biological membranes: is homeoviscous adaptation the explanation? Annual Review of Physiology 57:19–42.

Hazel, J. R., and E. E. Williams. 1990. The role of alterations in membrane lipid composition in enabling physiological adaptation of organisms to their physical environment. Progress in Lipid Research 29:167–227.

Hochachka, P. W., and G. N. Somero. 2002. Biochemical adaptation, mechanism and process in physiological evolution. Oxford University Press, Oxford.

Hoffmann, A. A., S. L. Chown, and S. Clussella-Trullas. 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? Functional Ecology 27:934–949.

Hoffmann, A. A., and C. M. Sgro. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hom, E. F. Y., and A. W. Murray. 2014. niche engineering demonstrates a latent capacity for fungal-algal mutualism. Science 345:94–98.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Horton, D. E., N. C. Johnson, D. Singh, D. L. Swain, B. Rajaratnam, and N. S. Diffenbaugh. 2015. Contribution of changes in atmospheric circulation patterns to extreme temperature trends. Nature 522:465–469.

Huey, R. B., C. Deutsch, J. Tewksbury, L. Vitt, P. Hertz, H. Álvarez Pérez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B 276:1939–1948.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology and Evolution 4:131–135.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist 19:357–366.

Hughes, T. P., K. D. Anderson, S. R. Connolly, S. F. Heron, J. T. Kerry, J. M. Lough, Andrew H. Baird, et al. 2018a. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, et al. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373–377.

Hughes, T. P., J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, et al. 2018b. Global warming transforms coral reef assemblages. Nature 556:492–496.

Huntingford, C., P. D. Jones, V. N. Livina, T. M. Lenton, and P. M. Cox. 2013. No increase in global temperature variability despite changing regional patterns. Nature 500:327–330.

IPCC (Intergovernmental Panel on Climate Change). 2014. Climate change 2014: synthesis report. Contribution of working groups i,
Schulte, P. M., T. M. Healy, and N. A. Fangue. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integrative and Comparative Biology 51:691–702.

Screen, J. A. 2014. Arctic amplification decreases temperature variance in northern mid- to high-latitudes. Nature Climate Change 4:577–582.

Sears, M. W., E. A. Riddell, T. W. Rusch, and M. J. Angilletta. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the USA 111:5266–5270.

Sardón, J. P. 2007. The 2003 heat wave. Eurosurveillance 12:11–12.

Shaw, T. L., and K. R. Lips. 2007. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 151:86–96.

Shaw, T. L., and K. R. Lips. 2009. Ecosystem responses to climate change using thermal performance curves and photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. Proceedings of the National Academy of Sciences of the USA 106:851–856.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2015. Accelerating extinction risk from climate change. Science 348:571–573.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2016. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the USA 113:10150–10155.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2017. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the USA 114:11055–11060.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2018. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the USA 115:10585–10590.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2019. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the USA 116:6531–6536.

Shaw, T. L., K. R. Lips, and E. S. Vasseur. 2020. Tropical snake diversity collapses after widespread amphibian loss. Science 367:814–816.

Associate Editor: Jeremy W. Fox
Editor: Jennifer A. Lau