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Evolutionary rescue at different rates of environmental change is affected by trade-offs between short-term performance and long-term survival

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Abstract

As climate change accelerates and habitats free from anthropogenic impacts diminish, populations are forced to migrate or to adapt quickly. Evolutionary rescue (ER) is a phenomenon, in which a population is able to avoid extinction through adaptation. ER is considered to be more likely at slower rates of environmental change. However, the effects of correlated characters on evolutionary rescue are seldom explored yet correlated characters could play a major role in ER. We tested how evolutionary background in different fluctuating environments and the rate of environmental change affect the probability of ER by exposing populations of the bacteria *Serratia marcescens* to two different rates of steady temperature increase. As suggested by theory, slower environmental change allowed populations to grow more effectively even at extreme temperatures, but at the expense of long-term survival at extreme conditions due to correlated selection. Our results indicate important gap of knowledge on the effects of correlated selection during the environmental change and on evolutionary rescue at differently changing environments.

KEYWORDS

adaptation, climate change, evolutionary rescue, experimental evolution, temperature

1 | INTRODUCTION

Unless populations are able to relocate to more habitable areas, or have the ability to genetically adapt in situ, their numbers will decline and they will be pushed towards extinction by increasing temperatures (Bell & Gonzalez, 2009; Chevin et al., 2010; Lachapelle & Bell, 2012; McAllister et al., 1992; Thomas et al., 2004; Zwaan et al., 2008). As habitats free from anthropogenic impacts diminish and species are exposed to extreme environmental conditions that they may have no adaptation for (Bell & Collins, 2008;

Gomulkiewicz & Holt, 1995), genetic adaptation may be the only way to avert extinction (Bellard et al., 2012; Orr & Unckless, 2008).

Evolutionary rescue (hereafter ER) arises when a population recovers from a decline because of adaptation (Bell, 2012; Bell & Collins, 2008; Gonzalez et al., 2013). ER can occur in populations that have been negatively affected by environmental change, and when a population is able to survive either by using standing genetic variation or producing beneficial mutations that increase the population's fitness (Gomulkiewicz & Holt, 1995; Gonzalez et al., 2013; Killeen et al., 2017). As global climatic events become more unpredictable

(Grant, 2017) and environmental deterioration isolates populations from each other (Schiffers et al., 2013), it is important to understand how anthropogenic changes will impact extinction risks and Earth's biodiversity (Gonzalez et al., 2013; Lindsey et al., 2013).

Evolutionary rescue experiments produce more information on how individual populations can survive by producing beneficial evolutionary responses in changing environmental conditions (McDermott, 2019; Pauls et al., 2013) and how the rate of environmental change affects the likelihood of ER (Lindsey et al., 2013). Previously, ER has been studied by exposing populations to stress at varying rates of change in environmental conditions, for example salinity (Bell & Gonzalez, 2009), light (Bell, 2013), antibiotics (Lindsey et al., 2013) and temperature (Killeen et al., 2017). In general, experiments and theory suggest that higher population sizes, larger genetic variability and slower rate of environmental change increase the likelihood of ER (Carlson et al., 2014).

Correlated characters can have a strong effect on ER (Carlson et al., 2014) but this is rarely discussed (Boeye et al., 2013). In the framework of evolving at differentially changing environments, correlated characters can have a major influence on the outcome of ER. For example, a trade-off has been frequently found between growth and survival (e.g. Eschweiler & Christensen, 2011, Lewis, 2001, Zakrzewska et al., 2011, Biselli et al., 2020); therefore, slowly changing environments could lead to stronger selection on growth, as the population spends more time in a benign environment. This could improve the ability to grow efficiently also at extreme environments, at least for a short period of time. However, if there is a trade-off between growth and survival, increased growth could evolve at the expense of survival, which could be especially important at prolonged exposures to extreme conditions.

To test this, clonal populations of the bacteria *Serratia marcescens* spp. DB11 were exposed to stress by subjecting populations to steady increase in temperature at two different rates (slow = 1°C per day and fast = 2°C per day) to detect if the speed of environmental change affects on short-term performance (maximal growth rate and yield) at extreme conditions and long-term survival (extinction or ER) at extreme conditions. We used a pool of clones that were derived from an evolution experiment by Ketola and Saarinen (2015) and had experienced different environmental fluctuations over hundreds of generations. These treatments were: constant 31°C and two fluctuating conditions with abrupt or smooth fluctuations between 20–40°C, with smoother transitions having intermediate temperature of 31°C in between. Both fluctuations were fast, with 45 and 30 min between temperature changes, in abrupt and smooth treatments, respectively. Differentially evolved clones in constant and fluctuating environments could have led to adaptations that could be visible also in ER (Ketola et al., 2013; Lee & Gelembiuk, 2008; Räsänen et al., 2020; Saarinen et al., 2019). We hypothesized that (a) slower environmental change, in contrast to fast environmental change, will lead to improved ability for short-term performance measured by growth rate and biomass yield at extreme temperatures. (b) Moreover, if during slow environmental change there has been correlated antagonistic evolution on long-term survival, we would

expect that slow change would result in poorer long-term survival if environmental change has been slow, rather than fast. (c) If evolutionary background in adaptation to fluctuating environments is advantageous in a changing environment, we would expect to see that fluctuation-adapted strains perform better at extreme conditions.

2 | MATERIALS AND METHODS

Serratia marcescens spp. DB11 belongs to the family of *Enterobacteriaceae*, and it is a gram-negative, nonsporulating opportunistic pathogen and has a generation time of 26 min at 32°C (Jennison, 1935). It generally lives in temperatures between 5 to 40°C, and it is between 0.5–0.8 by 0.9–2.0 μm in size. The bacterium is globally distributed, and it has been identified as a cause of hospital infections (Hejazi & Falkiner, 1997) as well as a significant insect pathogen (Flyg et al., 1980).

2.1 | Evolutionary background of bacterial strains

The bacterial clones used in this work originate from an experimental evolution experiment (Ketola & Saarinen, 2015). This experiment started from a single clone, and that clone was reared in 31°C for two weeks to adjust it for growing conditions and then seeded to three Bioscreen C® (Oy Growth Curves Ab, Ltd, Helsinki, Finland) 100-well spectrophotometer plates with ten populations in each plate. These three plates were exposed to three different thermal regimes: constant 31°C, smooth fluctuating (30 min. intervals) temperatures between 24, 31 and 38°C, and abrupt fluctuating (45 min. intervals) temperatures between 24 and 38°C. Each of these thermal regimes lasted for two months and consisted of 27 renewals in total (renewals every 48 hr), and the estimated generation time was ca. 5.32 generations per renewal totalling ca. 144 generations.

2.2 | Evolutionary rescue treatment

To test how the speed of environmental change and the evolutionary background affect populations' ability to recover through ER, we subjected populations to two different rates of temperature increase. The environmental treatments were conducted with temperature-controlled Bioscreen C® spectrophotometers (Oy Growth Curves Ab, Ltd, Helsinki, Finland) to detect if the speed of temperature change (fast or slow) and the evolutionary background affect the likelihood of ER and the biomass yield.

To initiate the experiment, we used 90 *S. marcescens* spp. DB11 populations that had been kept in –80°C, in 1:1 v/v, 80% glycerol solution (Ketola & Saarinen, 2015) frozen in prerandomized order in Bioscreen 100-well plates. By utilizing cryoreplication, a procedure described by Duetz et al. (2000), we initiated the populations. In cryoreplication, the cryoreplicator's sterilized steel pins are pressed into frozen sample wells to obtain small samples from frozen populations.

When the replicator is pressed in liquid sterile media, small amounts of thawed bacteria will be transferred to medium. We grew the populations in NB medium for 24 hr before initiating each treatment to ensure a high enough bacterial density. As the samples had been prerandomized when frozen for storage, the wells on the original 100-well spectrophotometer plate (Bioscreen C® Oy Growth Curves Ab, Ltd, Helsinki, Finland) contained bacteria populations ($N = 90$) from the three different thermal treatments in random order (Ketola & Saarinen, 2015).

We grew the populations in NB medium in rising temperatures in the spectrophotometers and subjected the populations either to slow or fast thermal increase. Both spectrophotometers had a starting temperature of 31°C and final temperature of 39°C (defined prior this experiment). The duration for both treatments was nine days. In the slow treatment, the populations were subjected to a daily 1°C increase in temperature for the first nine days (temperatures increased from 31 to 39°C). In the fast treatment, the populations were first reared at the steady temperature of 31°C for five days after which the temperature increased 2°C daily. Both treatments were run simultaneously to avoid any bias caused by day effects in measurements. In the fast treatment, the first 5 days are merely to make sure that populations in both treatments are living in similar conditions and are not getting any selective advantage, for example due to light, air conditions. Moreover, the first 5 days are not giving the populations in the fast treatment any selective advantage as the populations have been reared in 31°C prior this particular experiment.

We renewed the Bioscreen plates at daily (24 hr) intervals by transferring samples of bacteria (12.5 μl, ThermoFisher Scientific Matrix™ eQualizer 125 μl 12 Channel Electronic Pipette, Waltham, MA USA) to new plates containing preheated NB medium (to avoid heat shocks). Every day, we rotated the plates between two Bioscreen spectrophotometers and adjusted the temperatures accordingly. During the experiment, bacterial biomass growth was observed every five minutes. In total, ca. 5 generations a day and 45 generations in total were reached during the experiment, and the number of generations was limited by available resources (Bennett et al., 1992).

2.3 | Measurement of short-term performance

After reaching 39°C, we transferred 12.5 μl samples to two, instead of one spectrophotometer plate yielding four measurement plates for the final measurements. Two plates, one from slow and one from fast treatment, were placed on 39.5°C. Similarly, two plates were placed on 40.0°C. These two temperatures were determined by pre-experiments to yield extinction with high likelihood and bringing up the differences in strains' capability for ER. Our analyses are based on measured maximal growth rate and yield over first day at final measurement temperatures, which measures how performance at short timescales at extreme temperatures is affected by the speed of experienced environmental change.

2.4 | Measurement of long-term survival

After four days, with daily renewals of resources at these temperatures, we lowered the temperatures back to the starting temperature of 31°C for two days to observe if the populations had become extinct or if they had just become dormant due to inhospitable thermal conditions (Jones & Lennon, 2010). This measurement indicates how long-term survival at extreme temperatures is affected by the speed of environmental change.

2.5 | Data analysis

The raw Bioscreen C® (Oy Growth Curves Ab, Ltd, Helsinki, Finland) growth measurement data were first processed with RStudio (RStudio Team 2015, version 3.6.1) for calculating growth rates and yields. From the raw growth data, we calculated maximal growth rates and maximal biomass yield based on the method previously described in Ketola et al., 2013. In short: the fastest instantaneous growth rate was determined by fitting linear regression slope on a sliding window of 30 data points (equalling 150 min of growth) on ln-transformed OD data. From the resulting data, the fastest increase in biomass per time unit was chosen to represent maximal growth rate and the highest average biomass was chosen to represent maximal biomass yield. Both maximal growth rate and maximal biomass yield are important for bacterial fitness. Bacterial growth rate indicates how fast bacterium can utilize the resources and is utmost important when competing for scarce resources. Biomass yield in patch cultures, that is with finite resources, indicates how well bacteria can convert available resources to biomass. Both of these could be indicative of bacterial fitness (Ketola et al., 2016; Novak et al. 2006). Since our methodology for detecting growth and amount of bacterial biomass is dependent on the turbidity of the samples, the very low population sizes at extreme temperatures at day 10 are still measurable, yet the days 11–13 prevent accurate estimation of growth rate and yield and also our ability to distinguish if populations perished. Therefore, we designed our experimental measurements such that we could measure the number of populations that survived at extreme conditions. An ability to start growth, at benign conditions, after four days at extreme conditions was used to reveal if strains had gone extinct or survived. Population was scored as extinct if it failed to reach an optical density of 0.2. In comparison, populations that were alive reached an OD (600 nm) up to 1.5.

Three statistical analyses were performed, one for each trait (growth rate, biomass yield and survival). All analyses contained the same explanatory variables: rate of temperature change (fast and slow) and evolutionary background (constant temperature, smooth fluctuations and abrupt fluctuations). The inoculum size was set as a continuous covariate to control the deviations in starting population size (in growth rate and biomass yield). Since the data contain measurements from bacterial clones that were evolving in same populations, we controlled the arising nonindependency by including population ID where bacterial clone originated from, as a random factor. Maximal biomass yield was tested with linear model, but the likelihood of extinction was

	Growth rate			Biomass yield		
	Chisq	Df	Pr(>Chisq)	Chisq	Df	Pr(>Chisq)
Temperature: 39.5°C						
(Intercept)	370.942	1	<0.001	432.305	1	<0.001
Evolutionary background	0.336	2	0.846	0.218	2	0.897
Rate of environmental change	61.585	1	<0.001	85.194	1	<0.001
Inoculum size	434.522	1	<0.001	714.429	1	<0.001
Temperature: 40.0°C						
(Intercept)	327.771	1	<0.001	234.120	1	<0.001
Evolutionary background	2.142	2	0.343	1.912	2	0.385
Rate of environmental change	37.651	1	<0.001	45.102	1	<0.001
Inoculum size	383.907	1	<0.001	480.389	1	<0.001

TABLE 1 Results of mixed model exploring determinants of short-term performance, measured as maximal growth rate and biomass yield at 39.5 and 40.0°C

Note: Interaction between evolutionary background and evolutionary rescue treatment did not improve model fit in any of the models and is not included in the final models.

tested with generalized linear model with binomial model and logit link. Analyses were done using the linear mixed-effects models lme4 package (Bates et al., 2015, version 1.1–21) in RStudio (RStudio Team 2015, version 3.6.1). In all analyses, the analyses were conducted on main effects of treatment and evolutionary background, as inclusion of interaction between these variables did not increase the model fit.

To test how growth and yield at day 10 affected extinction probability at day 14 at 39.5°C, we used logistic model explaining extinction risk by performance traits (maximal growth rate and biomass yield, both z-standardized). Both traits were tested separately in model where inoculum size and random effect of population identity were taken into account.

3 | RESULTS

3.1 | Short-term performance at extreme conditions

To explore how strains performed at the beginning of the four-day-long evolutionary rescue experiment, we followed the maximal growth rate and biomass yield at two extreme temperatures (39.5°C and 40°C).

Slow temperature change resulted higher growth rate at 39.5°C than fast temperature change (Table 1, Figure 1a). Growth rate was not affected by evolutionary background (Table 1) but larger inoculum size increased growth rate ($b = 0.0729$, $SE = 0.0035$, $df = 173.3$, $t = 20.845$, $p < .001$). Variance explained due to shared population identity was estimated to be 4.834×10^{-9} ($SD = 6.953 \times 10^{-5}$, residual variation = 4.975×10^{-8}, $SD = 2.230 \times 10^{-4}$). Slow temperature change was also associated with a higher growth rate at 40°C, than fast temperature change (Table 1, Figure 1c). Evolutionary background did not have an effect on growth rate at 40°C, but a

larger inoculum size increased growth rate at 40°C. ($b = 0.0568$, $SE = 0.0029$, $df = 172.7$, $t = 19.594$, $p < .001$). Variance due to population identity was estimated to be 8.592×10^{-10} ($SD = 2.931 \times 10^{-5}$, residual variation = 2.021×10^{-8}, $SD = 1.421 \times 10^{-4}$).

The strains that had experienced slow temperature change had clearly higher biomass yield than the strains that had experienced fast temperature change at 39.5°C (Table 1, Figure 1b). Evolutionary background did not have an effect on biomass yield at 39.5°C. A larger inoculum size was found leading to a higher biomass yield ($b = 5.676$, $SE = 0.2124$, $df = 172.7$, $t = 26.729$, $p < .001$). Variance due to population identity was estimated to be 0.0000235 ($SD = 0.0048$, residual variation = 0.0002, $SD = 0.0135$). Slow temperature change increased also biomass yields at 40°C in comparison with strains that had experienced faster temperature increase (Table 1, Figure 1d). Evolutionary background had no effect on biomass yield whereas larger inoculum size led to higher biomass yield at 40°C ($b = 3.851$, $SE = 0.1757$, $df = 172.7$, $t = 21.918$, $p < .001$). Variance due to the population identity was estimated to be 4.818×10^{-6} ($SD = 2.195 \times 10^{-3}$, residual variation 7.256×10^{-5}, $SD = 0.0085$).

3.2 | Long-term survival at extreme conditions

To explore how differentially increasing temperatures affect survival at extreme temperatures, we conducted a four-day trial at 39.5 and 40.0°C in which resources were renewed every day, by transferring populations to fresh resources. During this time, population sizes were very low and nearly unobservable, pointing to the extinction of several strains. To test which of the strains were alive, we transferred strains to fresh resources and tested how many of them were able to recover when grown at 31°C. Since none of the strains revived at

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FIGURE 1 Effects of fast and slow environmental change on short-term performance and long-term survival. Whiskers indicate 95% confidence intervals
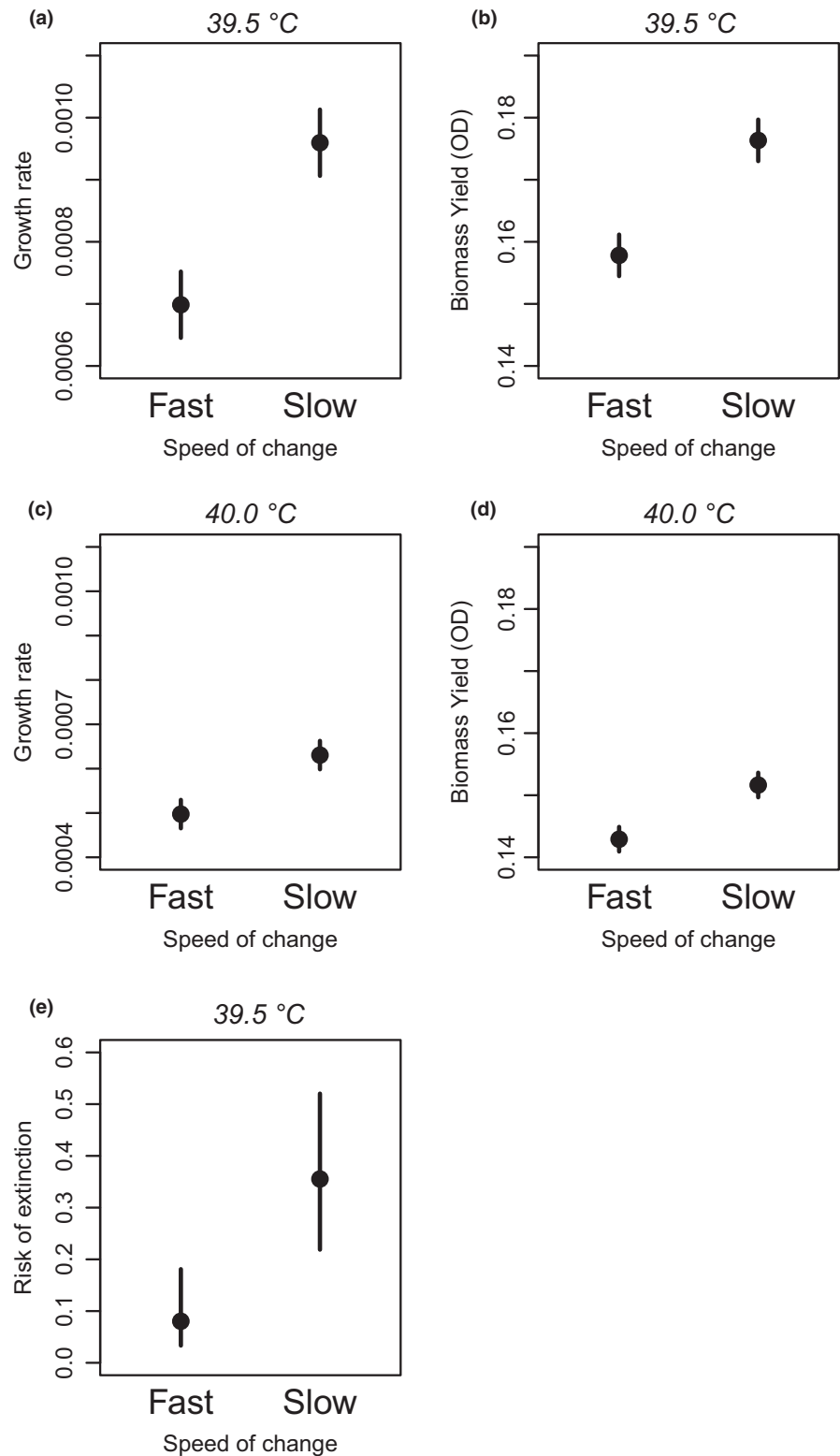
31°C, after spending four days at 40°C, we concentrate on the survival at 39.5°C. At 39.5°C, the strains that had experienced slow environmental change had clearly higher extinction risk than the strains that had experienced fast environmental change (Wald's $\chi^2 = 15.839$, $df = 1$, $p < .001$, Figure 1e). Evolutionary background had no effect on extinction risk (Wald's $\chi^2 = 1.993$, $df = 2$, $p = .369$). Variance due to population identity was estimated as 1.526 (SD 1.235).

3.3 | Trade-offs between survival and performance traits

In a stepwise logistic regression model exploring how extinction was explained by biomass yield and maximal growth rate, we found that across all treatments high yield (z-standardized) increased the risk of extinction ($b = 1.264$, $SE = 0.435$, $t = 2.906$,

$p = .0037$). This result was obtained from the model where non-independency of the measurements due to population identity ($\sigma^2 = 1.399$, $SD = 1.183$) and inoculum size at day 10 ($b = -349.962$, $SE = 89.262$, $t = -3.921$, $p < .001$) were taken into account (Figure 2a). In a similar analysis, growth rate indicated no effect on extinction ($b = 0.038$, $SE = 0.331$, $t = 0.113$, $p = .9097$; population identity: $\sigma^2 = 1.191$, $SD = 1.091$; inoculum size at day 10 $b = -142.8$, $SE = 67.78$, $t = -2.107$, $p = .0351$).

4 | DISCUSSION

As the effects of anthropogenic change and global warming accelerate, species are forced to find ways to adapt (Barnosky et al., 2011; Ceballos et al., 2015), which could be strongly related to the speed of environmental change (Gomulkiewicz & Holt, 1995) and be affected by correlational selection and past adaptations (Lee & Gelembiuk, 2008; Travisano et al., 1995). Here, we studied if the rate of environmental change, correlated selection and past evolutionary changes affect the probability of evolutionary rescue.

Our results indicated that a slow rate of environmental change resulted in higher short-term performance at extreme conditions (39.5 and 40.0°C) when measured with growth rate and biomass yield. Our results, thus, fall to a large pool of successful evolutionary rescue experiments repeating theoretical expectations, for example pinpointing the importance of population size and genetic variability in successful evolutionary rescue (reviewed in Carlson et al., 2014). In addition, slow environmental change has been found to increase the performance also at extreme conditions, and to lower the likelihood of extinction during the deterioration of environment (Bell & Gonzalez, 2011; Killeen et al., 2017), in comparison with fast environmental deterioration. Somewhat contrasting results were obtained when antibiotic resistance evolution was studied in similar settings. Despite a slower increase in antibiotic concentration, it increased the population size and lowered the extinction risk, during the course of experiment. Moreover, faster increases in antibiotic concentrations during the experiment yielded the strongest resistance at the end of the experiment (Lindsey et al., 2013; Perron et al., 2008).

When we explored the long-term survival of strains growing at extreme conditions (39.5°C) over four days with daily renewal of resources, we found out that those strains that had undergone fast change in environmental conditions had a lower extinction probability. When compared to the results of short-term performance, these are completely opposite and best explained by correlated selection. Growth traits (biomass yield and maximum growth rate) and survival are frequently found to be negatively correlated in many species (Lewis, 2001, Zakrzewska et al., 2011; Biselli et al., 2020) and very profoundly so in bacteria (Kussell et al., 2005; Taylor & Stocker, 2012; Velicer & Lenski, 1999). If traits were negatively genetically correlated, the stronger selection for growth at slowly changing environments would lead to strong corresponding losses in survival (e.g. Lynch & Walsh, 1998). Accordingly, we found strong negative relation between short-term performance (biomass yield)

and long-term survival. Such correlational selection has rarely been considered in evolutionary rescue literature (Carlson et al., 2014, but see: Boeye et al., 2013), but as shown here genetic correlations can be the mediators of an evolutionary trap, a phenomenon where evolutionary process itself produces genotypes of which future survival is jeopardized (Ferriere & Legendre, 2013). This naturally depends on if the short-term performance or long-term survival is the major fitness contributor. However, in this study, growth rate did not correlate with long-term survival. Possible mechanism for the trade-off is cellular mechanism for tolerating heat, such as heat shock proteins. Heat shock proteins have been found costly also in nonstress conditions (e.g. Kristensen et al., 2018). While tolerance mechanisms most likely cause resource losses also at the period of high growth, the surplus resources at the height of the exponential growth could still allow ample amounts of resources for growth and mask the underlying trade-off. However, since biomass yield reveals overall resource use efficiency over the duration of the growing period, the trade-off should be visible in biomass yield, but not in growth rate.

Previous evolutionary history of the strains has been suggested to play a role in future evolutionary trajectories. In particular, fluctuating environments could be possibly shaping invasion risks (Lee & Gelembiuk, 2008; Saarinen et al., 2019) and the emergence of pathogens (Arnold et al., 2007; Ketola et al., 2013). In evolutionary rescue settings, Gonzalez and Bell (2013) found two closely related species to differ in their responses. However, to our knowledge, no previous experiments have been carried out to find out if recent past selection pressures have an effect on evolutionary rescue. To do this, we utilized a pool of clones from an experiment where environments were either constant or fluctuated rapidly (Ketola & Saarinen, 2015). However, we found no signature of past evolution affecting evolutionary rescue. This is not an unexpected finding considering the rather small initial differences in strains in growth traits (Saarinen et al., 2019), and the overall impression from our previous experiments considering the overwhelming role of current conditions affecting on invasions (Saarinen et al., 2019, Räsänen et al., 2020, see also: Travisano et al., 1995).

According to our findings: whether evolutionary rescue should be considered successful or not or slow change considered beneficial or detrimental is severely affected by the duration of exposure to extremes. If long-term persistence reflects the selective conditions better, it could be that actually species that had experienced faster change in environmental conditions are far better than those that experienced slower change, which is in contrast to the strongly held tenets of the benefits of slow changes in promoting evolutionary rescue.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13797.

DATA AVAILABILITY STATEMENT

Data are available at Dryad https://doi.org/10.5061/dryad.ngf1v hhtn.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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