Present environmental fluctuations drive species' competitive success in experimental invasions

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Abstract

Climate change is presumed to increase both the number and frequency of fluctuations in environmental conditions. Fluctuations can affect the ecological and evolutionary processes that make species more successful competitors against other species. For example, fluctuating conditions can create selection pressures for traits that are profitable in adaptation to fast climate change. On an ecological timescale, environmental fluctuations can facilitate species competitive success by causing reductions in other species' population sizes. Climate change could then enhance species invasions into new areas if fluctuation-adapted invaders displace their native competitors in chancing environments. We tested experimentally whether fast environmental fluctuations, either past (on an evolutionary timescale) or present (on an ecological timescale) affect species competitive success. Bacteria evolved in either constant or fluctuating temperature were competed against the dominant invader *Serratia marcescens*, which had also evolved in either constant or fluctuating temperature. Moreover, the competition experiments were conducted in environments with similarly constant or fluctuating thermal conditions. The results showed that temperature fluctuations during competition, i.e. on an ecological timescale, made the invader more successful. Surprisingly, we did not find that the invaders' or its competitor species' evolution in fluctuating environments would have influenced the outcome of the competition. Our study highlights the importance of the present environmental fluctuations in promoting species' competitive success and potentially facilitating biological invasions.

Supplementary data:

Each row represents one competition experiment where one invader species (*S. marcescens*) clone that had evolved in constant or fluctuating temperature competed against one competitor species clone that had also evolved in constant or fluctuating temperature. The competition experiments took place in constant or fluctuating thermal environment. This design was repeated with three different competitor species (*P. putida, P. fluorescens and N. capsulatum*). In total we had 192 competition experiments. The competitive success of *S. marcescens* was calculated as the proportion of the invader colonies from the total colony count including also the competitor species colonies.

In our analyses, we had three fixed factors, the environment during competition, the evolution of the invader and the evolution of the competitor species, which all had two levels, constant and fluctuating temperature treatments. We fitted these three fixed factors, all their two-way interactions and the three-way interaction as explanatory variables. The identity of the invader clone, regardless of its evolution regime, and the identity of the competitor species were fitted as random factors. This was done to control for the non-independency of the observations, arising from the fact that the competitive success of the same invader clones was measured in two environments and against several competitor species.

We had a non-normal proportion data and the analysis included random effects, so we analyzed the data with generalized linear mixed model. We used a binomial error distribution and a logit link, and set the total number of colonies in a plate as a denominator to control for the total number of events in a trial. All analyses were run in SPSS (version 24.0, IBM-SPSS, Chicago, IL, USA). To find more information about the additional analyses, see the published article. The detailed descriptions of all used variables are given below.

Variable description:

Competition experiment

The running key number of competition experiments (sample plates).

Invader species

Serratia marcescens ssp. marcescens (ATCC® 13880™).

Competitor species

Pseudomonas putida (ATCC® 12633™), *Pseudomonas fluorescens* (ATCC® 13525™) or *Novosphingobium capsulatum* (ATCC® 14666™).

Invader's population, Competitor's population

We used one clone per replicate population (n = 8) for each bacterial species.

Invader's evolution, Competitor's evolution

In a previous study, populations were allowed to evolve separately for 79 days at constant (30°C) and in rapidly fluctuating (20°C-30°C-40°C, at two-hour intervals) temperature environments (Saarinen *et al*. 2018).

Environment during competition

We implemented competition experiments in two environments which matched the conditions during bacterial evolution, one with constant (30°C) and the other with fluctuating (20°C-30°C-40°C, at two-hour intervals) temperature.

Number of invader colonies, Number of competitor colonies, Total number of colonies

We counted the number of *S. marcescens* colonies and the number of its competitor species colonies in each sample after three days of competition. Competitive success of *S. marcescens* was calculated as the proportion of the invader colonies from the total colony count including also the competitor species colonies.

Invader clones' identity

The identity of the *S. marcescens* clone, regardless of its evolution regime.

Invader clones' inoculum size (OD), Competitor clones' inoculum size (OD)

Inoculum sizes reflect the optical density of bacterial cells in samples before the onset of competition experiments. Our additional analysis included clones' inoculum sizes as a covariate to control for the differences in starting cell densities.

Invader's maximum growth rate at 20°C/30°C/40°C/fluctuating temperature ,

Invader's maximum yield at 20°C/30°C/40°C/fluctuating temperature

We tested if the growth characteristics of the invader clones affected competitive success by fitting maximum growth rate and yield in four different temperatures (constant 20°C, 30°C, 40°C, and fluctuating 20°C-30°C-40°C, at two-hour intervals) as fixed covariates (additional data from Saarinen *et al*. 2018).