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Dormancy promotes coexistence in fluctuating environments

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Dormancy allows organisms to survive hostile conditions and is hypothesized to enable species to coexist in fluctuating environments. Although determining how species avoid extinction is critical to understanding the dynamics of natural populations, experimental work exploring *if* and *when* dormancy rescues populations from extinction remains rare. We conducted an experiment, where we grew two species of nematode at three temperatures. Strains of *Caenorhabditis elegans* had mutations altering their propensity to enter a dormant stage and *Caenorhabditis briggsae* was a single strain with a wildtype background. We used those empirical results to parameterize a model and simulate competitive outcomes in fluctuating environments between the two species. We show that upregulating the dormancy pathway rescues populations that would otherwise go extinct, thereby increasing coexistence between competing species. By leveraging the genetic tools available from a model system, this study provides experimental confirmation that dormancy specifically facilitates species coexistence and thereby promotes diversity. This study system could be used more expansively to explore the role of dormancy in species interactions.

Keywords: bet-hedging, buffered population growth, competition, dauer, dormancy

Synthesis

The ability of organisms to avoid conditions that could kill them is crucial for the long-term persistence of populations, but the relative importance of dormancy for biodiversity maintenance has remained uncertain. We use a novel experimental approach, harnessing *C. elegans* genetics to directly manipulate dormancy rates while holding other aspects of these worms' constant. We find support for the theoretical expectation that greater dormancy investment expands the range of environmental conditions where competing species can persist. We recommend broader adoption of the *C. elegans* system in empirical ecology.

Introduction

Avoiding sub-optimal conditions is crucial for populations to persist in the long-term, and organisms use a variety of strategies to do this. If organisms cannot always accurately predict future conditions, they can express a range of phenotypes that would succeed

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in different environments; this is the evolution of diversified bet-hedging strategies. Dormancy can be form of bet-hedging if the duration of halted development is distributed across offspring. Here, organisms forgo short-term reproductive success in favor of long-term persistence by reducing temporal variation in fitness (Slatkin 1974, Simons 2011). Dormancy is a strategy that is used by diverse organisms across the tree of life (Lubzens et al. 2010, Lennon et al. 2021). It is characterized by a reversible stage of reduced metabolic activity (Guppy and Withers 1999) and resistance to environmental conditions that would typically kill the active form of the organism (Radzikowski 2013).

In its simplest form, the dormant fraction of a population can be quantified as the ratio of 1) the arrested (dormant) phenotype that delays growth and reproduction for some period to 2) the active phenotype that develops and reproduces without delay. The frequency of dormant individuals in a population is not static but can evolve in response to local environmental conditions (Smith and Snell 2012, Graham et al. 2014, Rajon et al. 2014). Moreover, a shift to a dormant state can occur via a variety of mechanisms (Lennon and Jones 2011), but is usually triggered by changes in temperature (Stokes 1965), day length (Jones and Gilbert 2016), competition for limited resources (Golden and Riddle 1984) or predation (Tauber et al. 1986). Whatever the cue, theory predicts that organisms will invest more in dormancy as favorable conditions become less frequent (Cohen 1966, Ellner 1985) and that dormancy should play an important role in the persistence of competing species in fluctuating environments (Wisnoski and Lennon 2021).

Dormancy can impact the outcome of competition between competing species. For example, consider two species competing for a limited resource. If fitness differences are larger than niche differences, the species that produces more offspring on average will drive the other species to extinction, destabilizing coexistence. However, dormancy could modify this interaction through two mechanisms. First, investment in dormancy may trade off with the number of offspring produced that then reduces competitive differences in fitness (Adler et al. 2007, Chesson 2018), and second, dormancy offsets exposure to competition (Chesson and Warner 1981). Thus dormancy reduces the costs of competition in bad conditions relative to growth in good conditions (known as the storage effect) (Chesson and Warner 1981, Tuljapurkar and Caswell 2012). The net outcome of these forces working in concert determines coexistence outcomes.

While in theory, being able to produce environmentally resistant forms could help species escape harsh conditions and coexist, a direct link between dormancy and coexistence has not yet been demonstrated. Long-term demographic studies in nature have documented important relationships between environmental conditions and dormancy (Pake and Venable 1995, Gremer et al. 2016), and experiments have tested whether environmental variability affects competitive outcomes (Armitage and Jones 2019). However, neither set of studies isolated the contribution of dormancy itself to coexistence separate from the effects of genetic variation within populations and from environmental effects. This study fills that gap. While dormancy may theoretically permit coexistence among competitors, this outcome is not guaranteed in systems with real competition and life history parameters. We directly tested the effect of dormancy on coexistence by experimentally competing otherwise isogenic mutants that differ in their propensity to enter dormancy against a common competitor, thereby controlling the genetic and organismal background and the environment. We used that data to parameterize a two species consumer–resource model and simulated population growth across all 14 348 907 (3^{15}) distinct sequences for 15 resource pulses of three different temperatures to determine how dormancy affects competitive outcomes between the two species. This is the first empirical test of the theoretical prediction that dormancy plays an important role in the coexistence of competing species in fluctuating environments.

Material and methods

Study system

We used the species *Caenorhabditis elegans* and *C. briggsae* to explore the role of dormancy on coexistence. Although these species diverged approximately 20 million years ago (Cutter 2008), they appear virtually identical in morphology and have similar life-histories and ecologies (Supporting information). Both species have global distributions and have been found to co-occur on the same rotting fruit (Félix and Duveau 2012). Although most *Caenorhabditis* species have separate sexes (gonochoric), these two species are self-fertilizing hermaphrodites (with rare males). Lab experiments with wild isolates revealed that *C. elegans* outcompetes *C. briggsae* at a cold temperature (15°C) while *C. briggsae* outcompetes *C. elegans* at a warm temperature (27°C) (Félix and Duveau 2012, Oro 2020). *Caenorhabditis* nematodes have two alternative routes to adulthood. Under favorable conditions, they quickly progress through four larval stages to become reproductive adults. If environmental conditions are unfavorable (i.e. high heat, low food or crowding), they can enter a metabolically-quiescent, long-lived, dormant larval stage called dauer, until conditions improve and they can resume their development to adulthood (Golden and Riddle 1984). In the wild, they cycle through episodes of rapid population growth and dispersal consuming bacteria on a new rotting fruit until the food runs out or it becomes too crowded and then entering dauer until they reach a new fruit.

Worm strains

We selected *C. elegans* strains from the *Caenorhabditis* Genetics Center with mutations in the dauer (dormancy) network (Table 1). The strains were either wild-type (hereafter WT), had an increased propensity to enter dauer (hereafter increased dauer), a decreased propensity to enter dauer (insensitive to the dauer-producing pheromone that is used

Table 1. Species, strain and dauer manipulation used in the experiment. 9 treatments × 3 temperature × 4 replicates = 108 plates total.

Species	Strain	Dauer manipulation
Caenorhabditis elegans	CGC59 (WT)	Wild type
Caenorhabditis elegans	PY7505	Increased dauer
Caenorhabditis elegans	DR476	Dauer defective (Knock Out)
Caenorhabditis elegans	JT646	Insensitive to dauer pheromone
Caenorhabditis briggsae	JU1018	Wild type-myo-2-RFP

CGC59 – *C. elegans* gnnr-7(umn3[LoxP +myo2::GFP +NeoR+LoxP])
PY7505 – *C. elegans* oyls84 [gpa-4p::TU#813 + gcy-27p::GFP + unc-122::DsRed]
DR476 – *C. elegans* daf22(m130)
JT646 – *C. elegans* hid-3(sa646)
JU1018 – *C. briggsae* mfls42 [Cel-sid-2 +Cel-myo2::DsRed]

to sense population density; hereafter insensitive to pheromone), or were dauer defective (Table 1 for strain descriptions). The worm species are morphologically indistinct, so we selected *C. elegans* strains that had a green fluorescent protein (GFP) tag and fluoresced green (Table 1, Supporting information) and the single *C. briggsae* strain we selected, JU1018, had a wild-type AF16 background tagged with a red fluorescent tag, *myo-2* DsRed, so it fluoresced red (Table 1, Supporting information). Until the experiment began we maintained all strains at 22°C under standard laboratory conditions (on NGM-lite plates, transferring worms as necessary to plates with fresh *E. coli*) (Brenner 1974).

Experimental methods

Monoculture experiments

We conducted monoculture and heteroculture growth assays for each of the four *C. elegans* strains with *C. briggsae* (Table 1) at three temperatures (15, 22, 27°C). A schematic diagram summarizing the experimental design is available in the Supporting information. In what follows, we report the results using the single species parameters; the outcomes of both sets of parameters are qualitatively similar (Supporting information), except that contamination/counting error made the estimate of the probability of entering dauer unreliable in the heterospecific dauer knockout treatment. However, parameterizing competition models with data from monoculture experiments is consistent with microbial studies of coexistence which use single species parameters. For each experimental condition, four replicate populations were grown on 9 cm NGM-lite (2% agar) plates seeded with 500 µl freeze dried *E. coli* OP50 lawn from Lab TIE B.V. (Netherlands) (Supporting information). As a result, for the monoculture experiment, we had five strains crossed by three temperatures with each strain replicated four times (5 × 3 × 4 = 60 plates). We began the population with two L4 hermaphrodites. The L4 stage was used so that eggs had not developed before the application of the temperature treatment. Individuals were collected from the stock strain population using a platinum wire worm pick that we sterilized using a Bunsen burner flame.

To estimate population size, we counted individuals using a Zeiss SteREO Discovery V8 dissecting microscope with an Achromat S 1.0X 63 mm objective with a X-Cite 120Q fluorescence lamp and a base for epi- and trans-illumination (Schott A20960.1 LED). We subsampled the plate by photographing ten circular regions of the plate (Supporting information) (diameter = 7 mm), so that in total we sampled ~ 5% of the area of each plate each day (twice a day for worms grown at 27°C, because the population increased in size rapidly). We continued to measure the population size until the worms had exhausted all resources by eating all the available *E. coli*. We counted all adults in the subsamples from the photographs. We used the *all_splines* function in the R package 'growthrates' (Petzoldt 2018) to estimate the maximum per capita growth rate ($\boldsymbol{\mu}_{max}$) by fitting non-parametric smoothed splines (smoothness manually adjusted to 0.5) to the exponential part of the growth curve and extracting the maximum rate of change. We calculated the maximum population size for each [strain × competition × temperature] combination.

Dauer worm recovery

When the populations had exhausted all the resources on the plate, all non-dauer worms were doomed. To ensure that all remaining worms survived past the dauer decision (either into L3 and beyond or into dauer), first we waited for at least 48 hours after the populations had consumed all the *E. coli.* Second, we washed all the worms off each plate and into a 1% aqueous sodium dodecyl sulfate (SDS) solution which kills non-dauer worms (Cassada and Russell 1975). Next, we thoroughly mixed the solution containing dauer worms and plated equal volumes onto each of three new plates containing a lawn of 200 µl of *E. coli.* These plates were placed at either 15, 22 or 27°C (Supporting information). Switching the environment accounts for environmental variation and the role of the past environment on the rates of leaving dauer in the current environment. We photographed the plates using the same methods as described above 24 and 48 h after replating the dauer worms with new resources. The maximum number of dauer worms recovered from a single plate was 489. In total, we counted 55 871 worms across the population growth and recovery components of the experiment. In our experiments, a small fraction of dauer defective worms were recovered after the SDS treatment, suggesting either that this strain produces dauers at a very low rate or a small amount of experimental error. The rates are not large enough to affect the subsequent dynamics (Supporting information).

Model simulations

We formulated a differential equation model for two species undergoing exponential population growth while competing for a single resource at three temperatures. This model was designed to allow for abrupt changes in the state variables [population size, resources]. In our case the model represents nematode colonization and population growth in a rotting fruit, followed by dispersal and colonization of a new fruit. Each model simulation follows the fate of a single two-species community that grows until resources run out (Eq. 1–2), which triggers dispersal to a new resource. Only dauer worms successfully disperse, and so after each dispersal event the population sizes (X_1 and X_2) start from the number of dauers of each strain or species generated from the previous colonization (Eq. 3). Upon colonization of a new rotting fruit, the resources are renewed. For each strain and temperature, we calculate a dormancy parameter (h) from the experimental data by calculating the fraction of the population in dauer (Supporting information). This was done by dividing the number of living dauer worms that we counted when food ran out by the maximum population size. This gives us the fraction of the population that is in dauer at each dispersal event, which we held constant through time. We explored all possible temporal sequences of the three temperatures in the simulations over 15 successive colonization events, called pulses below (3^{15} or 14 348 907 sequences). Within pulse dynamics are modelled using continuous time, while the pulse (period) is discrete. The model can be written as follows:

The change in number of adults of species i at time step t (days) in growth period p (discrete; sequence of new environments representing fruit) characterized by environmental condition (temperature) e is given by

$$dX_i(t,p)/dt = \mu_{\max,i,e} X_i(t,p) - X_i(t,p) \times h_{i,e} \quad (1)$$

for all $t > 1$, where $\mu_{\max,i,e}$ and $h_{i,e}$ are the species- and temperature-specific maximum growth rate (24 h) and dauer production (proportion), respectively. Each simulation starts with two individuals of each species, therefore $X_i(1,1) = 2$ for all i.

The change in availability of the resource (µl *E. coli*) is given by

$$dR(t,p)/dt = R_0 - \sum_{i=1}^{n} Q \times X_{i,e}(t,p) \quad (2)$$

for all p. Q is the resource consumption per adult individual, assumed to be independent of temperature, species and strain. We estimated Q once for all strains by dividing the experimental resource concentration (500 µl *E. coli*) by the maximum population size, which worked out to be approximately 4.0 µl *E. coli* per worm. In all cases the initial resource concentration, R_0, is set to 5000.

When resources are depleted, only dauer worms survive, and we start a new growth pulse, with starting population sizes for each strain equal to that strain's dauer production in the final time step of the previous growth pulse:

$$X_i(1,p) = h_{i,e} \times X_{i,e}(t_{crit}(p-1), p-1) \text{ for all } p > 1, \quad (3)$$

where t_{crit} is determined by solving for the time at which $R \leq 0$ in growth period p in Eq. (2).

We simulated temperature variation using a recursive function that trifurcates such that the temperature can take one of three values (15, 22 or 27°C at each new pulse of resources (colonization event). The temperature dependency of the model is incorporated through the direct effect of temperature on 1) μ_{max} and 2) h. Simulations were run until one species went extinct or reached 15 pulses, whichever came first. At the end of each simulation, we tallied one of three possible outcomes: *C. elegans* persisted, *C. briggsae* persisted or coexistence (both species persisted).

Because populations grow exponentially, instead of solving the ODEs, we used the *uniroot* function (package: 'stats' (www.r-project.org)) to solve for the time at which the resources R go to zero and then calculated the population growth of each species and the dauer fraction up to that time. This is equivalent to but quicker than solving the ODE, which speeds the computation up to over 3^{15} simulated pulses. After the resources go to zero, the non-dauers die, the dauers become reproductive adults, the resources are replenished, the new temperature is set, and the simulation proceeds.

Results and discussion

Our experiment confirmed the impact of temperature on the growth rates of different *Caenorhabditis* populations (Fig. 1). Resources were exhausted more rapidly at higher temperatures. On average it took 13.9 ± 1.5 days in the 15°C treatment, 9.00 ± 0 days for the 22°C and 7.03 ± 1.22 days in the 27°C respectively (Fig. 1, see the Supporting information for a full summary of the average days to starvation across strains). The effect of temperature on dauer worm production depended on the *C. elegans* strain (Supporting information, significant 2-way interaction, $p < 0.0001$). The dauer defective knockout strain produced essentially no dauer worms (Fig. 1D–F). The WT strain usually produced fewer dormant worms compared with the insensitive to the dauer pheromone strain. Dauer production was highest in the strain that has the dauer pathway upregulated, tending to be higher compared to their competitor *C. briggsae* at low and moderate temperatures. These results support previous work that documented that *C. briggsae* performs better at higher temperatures (Félix and Duveau 2012, Oro 2020).

Investment in dauer increases the range of conditions under which coexistence occurs. In constant temperature conditions several patterns emerge (Fig. 2–3, see https://labs.biology.ucsd.edu/rifkin/Projects/WormCoexistence/Visualization/index.html for an interactive exploration of the results). First, when investment in dauer is moderate (WT and insensitive to pheromone strains) and the temperature is low (15°C), *C. elegans* starts out with higher population growth compared to C. *briggsae*, suggesting that it might outcompete *C. briggsae*. However, the higher growth rate is

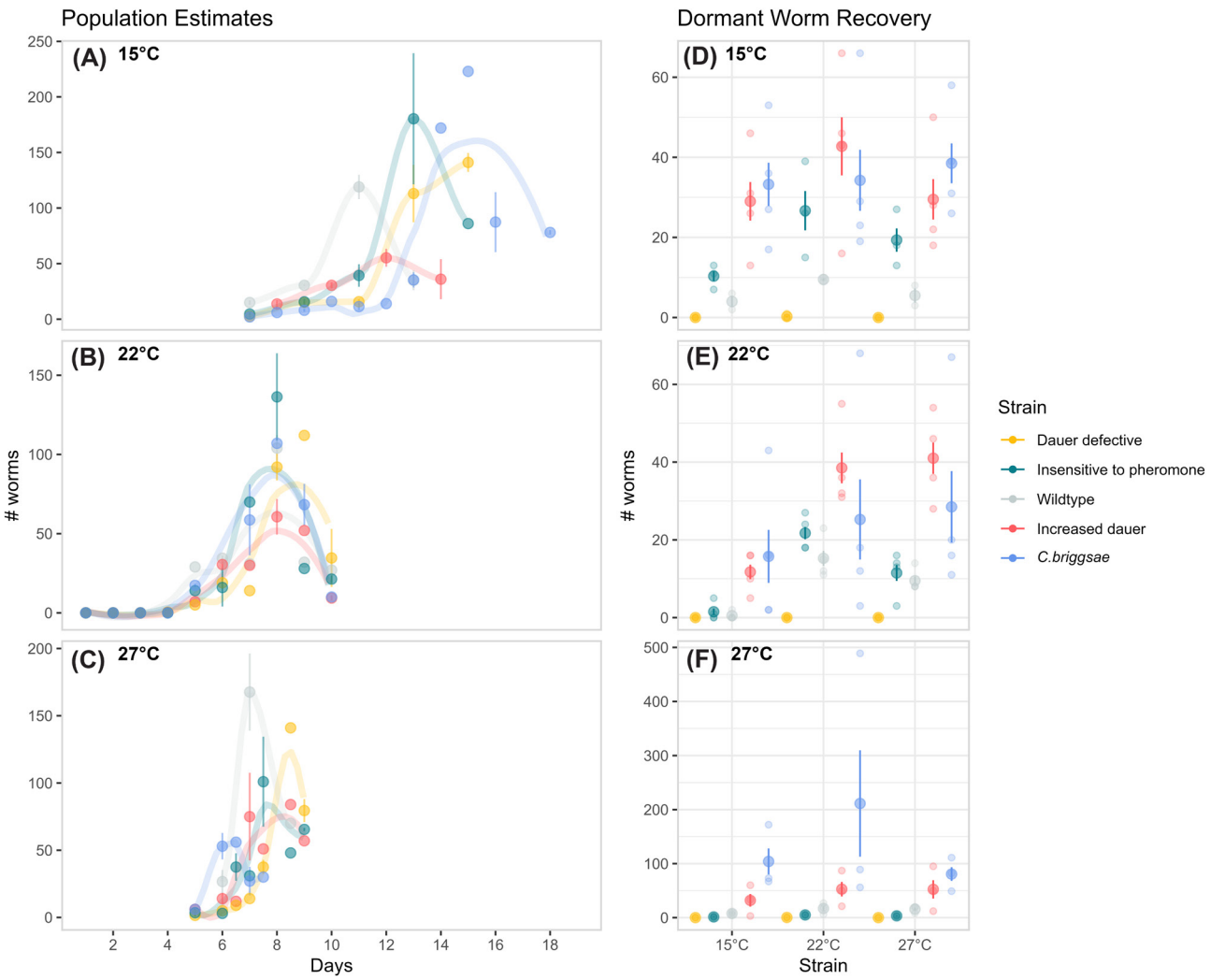

Figure 1. Means (± 1 SEM) of experimental results estimating maximum population size and dauer worm production across three temperatures for each strain. (A–C) Population size estimates over time for each strain at each temperature with a smoothed spline using a loess regression. (D–F) The average number of dauer worms that hatched at each possible temperature combination. For (D)–(F) we display both the means (± 1 SEM) and the individual replicates (smaller points). In all cases the temperature following the panel letter indicate the temperature at which the nematodes were originally grown in the experiment. In the recovery panels on the right, the x-axis displays the temperature at which the dormant worms were grown after being recovered. Please note that the y-axis scale differs among the panels.

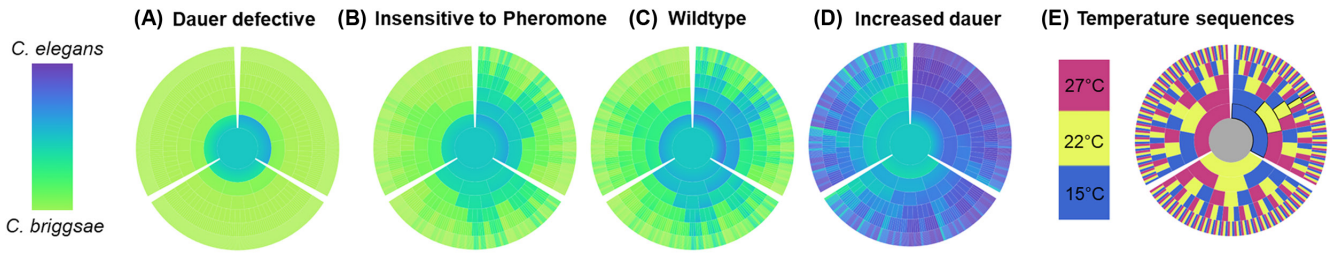

Figure 2. The ratio of *C. elegans* and *C. briggsae* populations after five pulses in the model simulation for the (A) Dauer defective strain, (B) Insensitive to pheromone strain, (C) Wildtype strain and the (D) Increased dauer strain. The disk at the right (E) represents the temperature trifurcation in the simulation, where all possible temperature sequences were simulated.

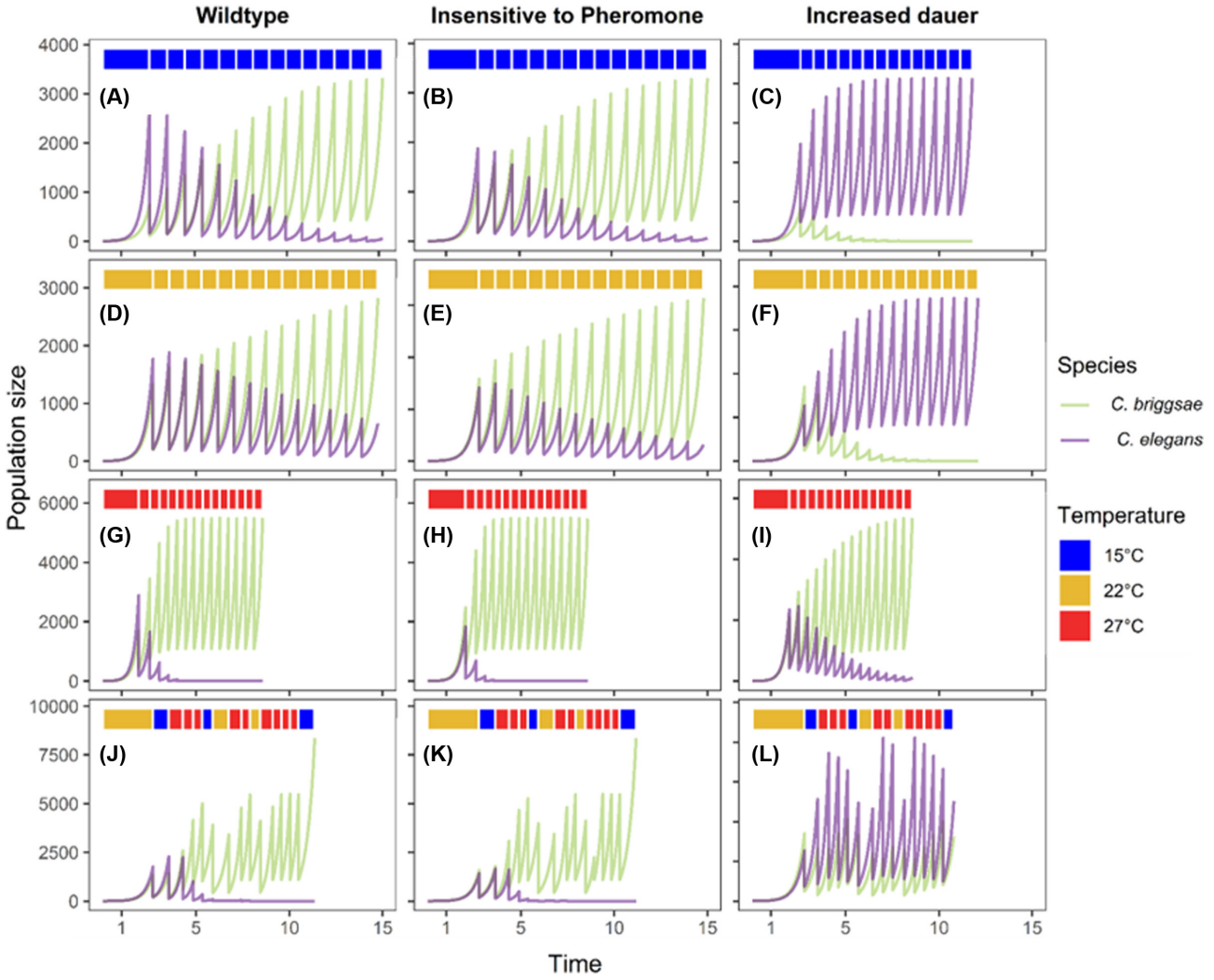

Figure 3. Examples of how both stable (top 3 rows) and fluctuating (bottom row) temperatures impact population dynamics. When temperatures are fluctuating the Wildtype (J) and Insensitive to pheromone (K) strains go extinct, but the increased dauer strain of *C. elegans* is able to coexist with *C. briggsae* (L). The rectangle colors denote the temperature of the environment and their widths indicate the duration of those conditions.

not enough to compensate for lower levels of dormancy, leading to the eventual extinction of both the WT and insensitive to pheromone strains after resources are exhausted and the worms need to disperse. Second, at intermediate temperatures (22°C), growth rates increase enough for WT and insensitive to pheromone strains to persist with *C. briggsae* through 15 pulses, although they will eventually go extinct. Finally, at high temperatures (27°C), the WT and insensitive to pheromone *C. elegans* strains, which have moderate dauer levels, cannot grow quickly enough to compete with *C. briggsae* and rapidly go extinct. The population dynamics are different for the high dauer strain. While the increased dauer *C. elegans* mutant also goes extinct when competing at 27°C, it drives *C. briggsae* extinct at 15 or 22°C. Interestingly, the high dauer mutant outcompetes *C. briggsae* at 15°C while the moderate dauer mutants (WT and insensitive to pheromone) go extinct. We note that the experimental results show that growth rates appear to be humped shaped or logistic, slowing as resources run out, as opposed to exponential as in our simplified model here. Future models that fit empirical population dynamics more closely, could further clarify the degree to which dormancy can alter coexistence outcomes. In any case, the results we obtained demonstrate that dormancy mediates the outcomes of competition even in stable environmental conditions.

Temporal variability in environmental conditions is ubiquitous in natural ecological systems. When we explored the role of temperature variation on coexistence outcomes, we found that higher variability in the sequence of temperatures led to more frequent coexistence (e.g. Fig. 3L). This result supports an important prediction from coexistence theory (Chesson and Warner 1981), which formalizes the conditions under which many similar species can live within communities, and has redefined how scientists view

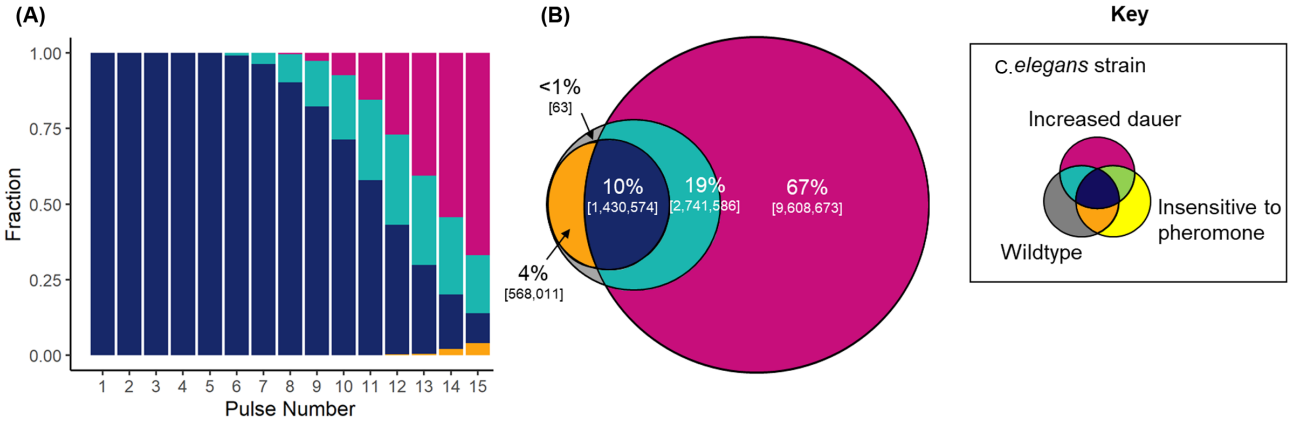

Figure 4. Coexistence outcomes from simulations. (A) The fraction of populations where *C. briggsae and C. elegans* coexist over time that is unique or shared across *C. elegans* strains for each temperature sequence. (B) Euler plot displaying the proportion of coexistence outcomes at the end of the simulation that are unique and shared among the strains. The bracketed numbers state the number of temperature sequences. We note that there were no environmental conditions that allowed only the insensitive to pheromone strain to persist. The key at the right specifies the unique and shared coexistence outcomes.

the maintenance of diversity (Grainger et al. 2019a, b). One ingredient for stable coexistence to occur is the temporal 'storage effect', which creates competition–environment covariance that introduces negative frequency-dependence to ecological dynamics. This fluctuation-dependent stabilizing mechanism allows rare species to recover and prevents dominant species from excluding others (Chesson and Warner 1981, HilleRisLambers et al. 2012). For this powerful coexistence mechanism to operate, 1) species competitive abilities must be correlated with environmental conditions, 2) no species can perform best under all conditions and 3) species must withhold (store) potential fitness until conditions improve.

Storage classically takes the form of a long-lived, environmentally resistant life history state (Chesson 1994, 2000, Cáceres 1997, Angert 2009), such as a cyst or seed, or a larval dauer worm in the case here. However, a long-lived state is not necessary for environment–competition covariance to occur. Moreover, the role of storage for the maintenance of diversity in natural systems remains uncertain, in part because natural systems tend to violate model assumptions, such as the absence on lags in environmental effects (Stump and Vasseur 2023). At the same time, recent theoretical advances have expanded the classic definition of storage to consider any mechanism that incorporates the effect of environmental conditions over time (Johnson et al. 2022). Our results show that when temperature fluctuates the WT and insensitive to pheromone *C. elegans* strains are outcompeted by *C. briggsae* (Fig. 3J, K). However, under the same fluctuating conditions, the increased dauer strain coexists with *C. briggsae* (Fig. 3L). Together these results show that, after controlling for genetic background, investment in dormancy can increase coexistence between competing species in fluctuating environments.

Higher investment in dauer formation increased the range of temperature sequences under which the two competing species could coexist (Fig. 4). In our simulations, the increased dauer strain coexisted in 67% of the 14 348 907 distinct temperature sequences, compared to only < 0.1% for the WT strain and none for the insensitive to pheromone mutant. With longer simulations the absolute numbers for each outcome would shift, but the main result would remain the same – higher dormancy leads to more coexistence. This is important because although selection on this trait should be strong, the optimum level of dormancy will depend on the structure of environmental conditions (Yamamichi et al. 2019). Our results suggest that, consistent with a field experiment with two chestnut weevil populations in France (Rajon et al. 2014), increased variation in environmental conditions will select for genotypes with a higher propensity to enter dormancy. This could shift the composition of populations and enable species that have dormant individuals to persist, especially if environmental conditions are correlated through time (Di Cecco and Gouhier 2018). As climate change eliminates millions of species in the coming decades, our results raise an important question that deserves further inquiry- will species that have a dormant form be more resilient to global change? This question becomes even more compelling since dormancy has been found to be more important for rare species in microbial lake communities (Wisnoski and Lennon 2021). Together, this suggests that dormancy could be part of the puzzle for determining the 'winners' and 'losers' of climate change.

In conclusion, by using genetic resources available in model systems but absent in natural ecological communities, we tested the longstanding hypothesis that dormancy in itself promotes coexistence in temporally variable environments. Although our approach – a controlled laboratory experiment paired with model simulations – simplifies the complex mechanisms operating in nature, we nonetheless demonstrate that dormancy can play a large role in promoting coexistence between species. We encourage ecologists to explore the role of dormancy in their study system and to consider using *Caenorhabditis* to test the role of dormancy for the maintenance of diversity.

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Author contributions

Natalie T. Jones: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Visualization (equal); Writing – original draft (lead). **Joanna D. Bundus**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – review and editing (supporting). **Jonathan B. Shurin**: Conceptualization (supporting); Funding acquisition (equal); Writing – review and editing (supporting). **Scott A. Rifkin**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9p8cz8wk3 (Jones et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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