Special issue:

"The role of plasticity in phenotypic adaptation to rapid environmental change"

Phenotypic plasticity in response to climate change:

the importance of cue variation

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Supplementary materials

Box S1: Empirical evaluation of cues for plasticity

Plasticity cues can be very difficult to identify in empirical systems. By directly manipulating the environment, experimental work can determine which specific cue triggers phenotypic expression (e.g. defenses induced by predator "smell", or kairomone [1]). A particular advantage of such laboratory experiments is that they allow cues to be identified by decoupling them from (i) other environmental variables that may covary with them *in natura*, and (ii) other environmental variables that drive selection on the plastic trait. For example, experimental work on shade responses in plants allowed disentangling the effects of spectral quality (red/far red ratio, an indicator of the presence of competitors) and the amount of light (photosynthetically active radiation, signaling neutral shade e.g. from a rock [2]). However, adequate manipulation of the cue may be more complex than anticipated, because the timing and pattern of variation in the environment is also important in eliciting phenotypic responses. For example, laying date in a Dutch great tit population is more sensitive to patterns of temperature than to average temperature per se [3,4] and so are thermal reaction norms of parasitic wasps [5]. Failing to integrate environmental variability in experiments may lead to poorly evaluate responses to an environmental factor [6].

In nature, in contrast, the difficulty is to assess which environmental variable is actually used by the organisms. This requires long term (\geq 20 years [7]) correlative studies. Many studies of phenotypic plasticity in the wild use a priori knowledge [7], others evaluate which environmental variable explains the highest proportion of phenotypic variance. For climatic predictors (e.g. in studies of phenology), the most common method to achieve this is to use sliding window analyses. But until recently and the development of statistical packages such as climwin [7,8], there was no formal statistical framework to assess the validity of detected cues. The recent methodological developments will allow assessing cues in the wild with more confidence, and will facilitate comparisons across studies. However, combining both experimental and *in situ* correlative approaches is required for a better understanding of each system. For example, an effect of mean temperature on laying date in great tits in the wild is known, but experimental work in the lab revealed later laying date in captivity than in the wild, suggesting the existence of other cues [9].

While organisms respond to complex environments that combine several environmental variables, a majority of studies only investigate one variable as a potential cue [7]. The use of simultaneous cues is extremely difficult to evaluate for wild populations, as this requires not only to define a set of potentially relevant variables that can be used as cues, but also to have access to long term data for a larger panel of environmental variables. These approaches are also very demanding in terms of power for data analysis, and are still rarely done in the wild (but see [10]).

Data summary, detailing for each population: forest type, time span over which data are available for blue tits and caterpillar phenology, and samples sizes for individual laying dates. The phenology of caterpillars is approximated by caterpillar frass mass collected regularly in coprometers, such that the day with the highest quantity of frass in each year corresponds to the date of the peak of caterpillar abundance of the year [11].

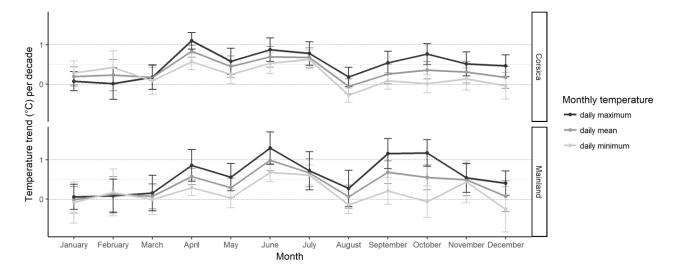
	D-Rouvière	D-Muro	E-Muro	E-Pirio
Forest type	Deciduous	Deciduous	Evergreen	Evergreen
Nb. mean laying date obs.	27	25	20	42
(year span)	(1991 – 2017)	(1993 – 2017)	(1998 – 2017)	(1976 – 2017)
Nb. females / nb. obs. of laying date	905 / 2040	752 / 1433	322 / 796	884 / 2120
Nb. caterpillar date obs.	10	25	17	31
(year span)	(1991 – 2002)	(1993 – 2017)	(2001 – 2017)	(1987 – 2017)
Caterpillar abundance	60.23 ± 8.33	2069.08 ± 447.70	517.86 ± 94.30	183.04 ± 23.63
(mean ± se, in mg/m²/day)				

Temporal trends in the four study sites for a) blue tits (laying date); b) caterpillars (date of peak abundance) and c) temperature (daily mean, daily maximum and daily minimum) during the reproductive period (from April to end of June) estimated over the period 1991-2017. Significant trends (p-value < 0.05) are in bold. Sample sizes are given in Table S1.

	<u>a)</u>	Laying date change (days per decade, ± se)	t-value	p-value	r ²	
 D-Rou	vière	0.10 (± 0.13)	0.08	0.94	-0.04	
	Muro	-0.61 (± 0.14)	-0.43	0.67	-0.04	
E-I	Muro	-3.57 (± 0.16)	-2.23	0.04	0.17	
E-	-Pirio	-3.15 (± 0.05)	-5.91	<0.0001	0.45	
		I				
	<u>b)</u>	Food peak change	t-value	p-value	r ²	
		(days per decade, ± se)				
D-Rouv	vière	-20.03 (± 11.51)	-1.76	0.12	0.19	
D-M	1uro	-2.99 (± 1.80)	-1.66	0.11	0.07	
E-M	1uro	-8.33 (± 3.93)	-2.12	0.05	0.18	
E-H	Pirio	-3.57 (± 1.35)	-2.65	0.01	0.17	
	I					
<u>c)</u>	Statis	tic Temperature change	t-valu	ie p-valu	ie r²	
		(°C per decade, ± se)				
Corsica	Mean	0.66 (± 0.2)	3.93	0.0005	0.36	
	Min	1.03 (± 0.3)	2.96	0.0067	0.23	
	Max	1.25 (± 0.3)	3.80	0.0008	0.34	
Mainland	Mean	0.61 (± 0.2)	3.92	0.0006	0.36	
	Min	0.91 (± 0.4)	2.55	0.0172	0.17	
	Max	1.10 (± 0.4)	2.68	0.0128	0.19	

Figure S1

Time trends of the daily mean (in dark grey), daily minimum (in light grey) and daily maximum (in black) temperature per month across years for Corsican sites (D-Muro, E-Muro and E-Pirio) and the mainland site (D-Rouvière) for the 1991-2017 period. Values are slopes of a regression of temperature against year as a linear trend, estimated for each statistic (mean, max and min) for each month (± se).



Box S2: Methods: Details of sliding windows analyses

General procedure

In order to estimate the period during which climate most strongly influences the phenology of blue tits and caterpillars, we implemented sliding window analyses using the package climwin [7,8]. Correlation between mean laying date or caterpillar date with temperature and rainfall was tested across years for every period of more than 1 day in all years. For mean laying date of blue tits, data on known second clutches were removed, and individuals with laying dates later than 30 day after the first laying date of the year in each population were eliminated from the data sets. We tested several summary statistics for both temperature and rainfall: daily mean, maximum, minimum temperature during each period for all populations. We defined Extreme Climatic Events (or ECE) as the highest 5% of the distribution of a climatic variable over a period of reference [12]. We chose this reference to be the period of sensitivity to mean temperature (population specific best model, see below) for the years 1991-2017. For each climatic parameter, we tested for both linear and quadratic reaction norms. We allowed the window to overlap with the period of reproduction and development (respectively for birds and caterpillars), as a way to assess whether plasticity is predictive, i.e. if the best cues are found before and not during the breeding season.

Among all tested combinations of climate parameters, summary statistics, and relationship functions, we retained the models that best predicted the among-year variation in the mean phenotype for each population and species. Model choice was based on three indicators of the ability of the models to explain the among-year variation of the phenotype:

- i) The ΔAIC is the difference between the Akaike Information Criterion (AIC) of a given model and that of a basic model including an intercept only, hereafter the base model. This difference estimates the ability of the focal model to explain the temporal variance in the mean phenotype, as compared to the base model. The lower the ΔAIC , the higher the explicative power of the detected cue windows.
- ii) The critical probability P_c represents the probability to detect the best windows as a signal just by chance (akin to a p-value). We ran randomization procedure to test for the probability of false positives. We ran five simulation models using different randomizations of the mean phenotype across years (five randomisations are sufficient when using P_c according to robustness analyses of van de Pol et al. 2016) for each type of climate variable and summary statistics. The best model in these simulations with randomized datasets was chosen based on ΔAIC , and the probability of false positive in cue detection was then quantified as P_c . The smaller the P_c , the lower the probability that the cue window is detected just by chance.
- iii) The confidence set (%CI), quantifies the extent to which there are several models with very similar explanatory power, and thus provides a confidence interval on window limits. It is the percentage of all tested window models (for a given combination of climatic variable and summary statistics) that are required to reach 95% of the sum of all Akaike weights ($wAIC = exp(\Delta AIC)$). The models within this set compose the 95% confidence set of windows for the particular climatic variables tested. A small %CI suggests that only a few window models contribute to the cumulative predictive power of all tested windows, such that the best window is a reliable signal. The smaller the %CI, the higher the reliability of

the detected cues windows (opening and closing day of the windows are detected precisely).

The best model is the one that combines the smallest ΔAIC , the smallest %CI and the smallest P_c . In small datasets with lack of statistical power, %CI will increase. A window could have the best ΔAIC but a high P_c , meaning that the signal, despite strong statistical explicative power, is likely to be detected just by chance. In such a case, we evaluated the second best ΔAIC ; if the latter was associated with high P_c , we moved on to the third best ΔAIC , etc.and selected the first model in the list with low P_c . In small data sets, windows length will be sub-estimated [7]. For the summary statistic that best explains among-year variation of the phenotype, we estimated the median windows of models in the confidence set at 95%.

Note that mean temperature and the number of ECE are significantly positively correlated for blue tits windows in D-Rouvière ($r^2 = 0.68$), D-Muro ($r^2 = 0.48$) and E-Pirio ($r^2 = 0.26$), but not in E-Muro (p-value = 0.09, $r^2 = 0.12$).

Comparison of windows between populations

We wanted to test if the differences in best cue windows of blue tits from D-Rouvière and E-Pirio were significant. We focused only on these two populations because statistical power was high and equivalent in these populations, but much lower in the two other D-Muro and E-Muro populations. We computed the $\Delta AIC_{same windows}$ of a model where a single window was estimated for both populations. This was done by running the analysis on a pooled dataset including both the D-Rouvière and E-Pirio populations, with a fixed effect for population, in interaction with climate (i.e. mean temperature in window). Interactions between population and climate effects in the base line model allowed estimating different reaction norms of plasticity of laying date with respect to temperature for each population, but still using the same cue window for both populations. We then compared this model to the sum of ΔAIC of the best models (models 1) of D-Rouvière and E-Pirio estimated separately ($\Delta AIC_{different windows}$). Note that when the two populations are analyzed separately, compared to a model with no population effect, two additional parameters are estimated (open and close days for the second population). We thus added 2 points of ΔAIC in $\Delta AIC_{different windows}$ compared with the model ($\Delta AIC_{same windows}$). If the sum of $\Delta AIC_{different windows}$ is lower than the $\Delta AIC_{same windows}$, then estimating two different windows for the two populations provides a better fit to the data than a single common window, providing evidence that populations differ in their climate windows.

For comparison, the three sliding windows analyses are implemented with the same reference day (starting day of the sliding windows) equal to 1st July (however, results are consistent regardless of what reference day is used).Results from the sliding windows analyses show that,

$$\Delta AIC_{different windows} = \sum \Delta AIC = \Delta AIC_{D-Rouvière} + \Delta AIC_{E-Pirio} + 2$$
$$= -35.44 - 39.08 + 2$$
$$= -72.52$$

and

 $\Delta AIC_{same windows} = -19.98$

This clearly indicates that D-Rouvière and E-Pirio have different opening and closing days of temperature windows.

Consistency of information from local records of temperature (iButtons with temperature log every hour) and data from meteorological stations. Data from iButtons are available from 2009 to 2016 in D-Rouvière, and from 2013 to 2016 in E-Pirio, E-Muro and D-Muro. The congruence was estimated by regressions of the local average daily temperature (minimum daily temperature + maximum daily temperature / 2) from i-buttons placed near nest-boxes over corresponding mean daily temperatures from national meteorological stations (meteorological stations of Calvi for Corsican sites and Saint Martin de Londres for the D-Rouvière site). r^2 is the coefficient of determination. Significant slopes (p-value < 0.05) are in bold. Sample sizes are given in Table S1.

	In	itercept			r ²		
	Estimates (± se)	t-value	p-value	Estimates (± se)	t-value	p-value	
D-Rouvière	4.66 (± 0.40)	11.68	<0.0001	0.84 (± 0.02)	37.68	<0.0001	0.65
D-Muro	1.85 (± 0.39)	4.73	<0.0001	0.91 (± 0.02)	40.92	<0.0001	0.73
E-Muro	0.80 (± 0.46)	1.76	0.08	0.98 (± 0.02)	40.24	<0.0001	0.78
E-Pirio	-0.26 (± 0.25)	-1.02	0.31	0.96 (± 0.01)	68.19	<0.0001	0.84

Results from sliding windows analyses for blue tits and caterpillars. The best models are highlighted in red for each population. ΔAIC : Difference between the Akaike information criteria of the focal model and that of the base model (a model including the intercept only, see electronic supplementary material Box S2 for details about ΔAIC , P_c and %CI). Each line presents the best model from a sliding window analysis with the corresponding climate factors, statistics and function. Open and close day of time windows are counted backwards, starting from the reference day (= earliest date of phenotype + 30 day), consistent with the output format of the sliding windows implemented in climwin [7,8]. Note that in the main text, results are transformed to be expressed forward, with a reference Day 1= 1st January (see also table S5).

Sliding windows analyses 1 to 12 and ECE were implemented with the described combination of climate variable, summary statistics and reaction norm function. In the specific case of models "Cue1 + ECE", sliding windows analyses were implemented including in the base model the best temperature window estimated in model 1, in order to take into account the effects of annual mean temperature. However, in the table, we report for these "Cue1 + ECE" models the global ΔAIC i.e. the sum of the ΔAIC of the model 1 and of the model "Cue1 + ECE". The ΔAIC of all models in the table are thus directly comparable (with reference to a base model with intercept only).

						Blu	ie tits								
	Parameters	D-Rouvière						D-Muro							
Model	Cue	Statistic	Function	Threshold	Open	Close	ΔAIC	Pc	%CI	Threshold	Open	Close	ΔAIC	Pc	%CI
1	Temperature	Mean	Lin	-	98	24	-35.44	0.0007	2	-	78	16	-16.84	0.002	6
2	Temperature	Max	Lin	-	46	46	-11.37	0.52	77	-	49	48	-14.13	0.45	69
3	Temperature	Min	Lin	-	46	34	-22.54	0.0007	3	-	49	49	-12.60	0.47	75
4	Temperature	Mean	Quad	-	99	23	-35.12	0.002	2	-	4	1	-17.22	0.05	8
5	Temperature	Max	Quad	-	77	69	-11.25	0.90	71	-	289	276	-15.88	0.996	47
6	Temperature	Min	Quad	-	45	34	-21.26	0.002	3	-	4	2	-20.48	0.05	20
7	Rain	Mean	Lin	-	350	350	-8.60	0.90	93	-	199	195	-15.07	0.73	83
8	Rain	Max	Lin	-	350	350	-8.60	0.89	91	-	155	155	-13.91	0.55	81
9	Rain	Min	Lin	-	161	159	-9.66	0.82	94	-	155	155	-13.91	0.94	94
10	Rain	Mean	Quad	-	292	292	-12.20	0.83	82	-	348	348	-22.75	0.009	9
11	Rain	Max	Quad	-	351	350	-12.86	0.95	85	-	348	348	-22.75	0.002	14
12	Rain	Min	Quad	-	350	350	-12.13	0.82	94	-	348	348	-22.75	0.93	87
ECE	Temperature	Sum	Lin	13.36	96	40	-7.91	0.37	67	15.82	53	24	-5.72	0.58	77
Cue 1 + ECE	Temperature	Sum	Lin	-	-	-	-	-	-	-	-	-	-	-	-
	Parameters	•		E-Muro	•					E-Pirio					
Model	Cue	Statistic	Function	Threshold	Open	Close	ΔAIC	P_c	%CI	Threshold	Open	Close	ΔAIC	P_c	%CI
1	Temperature	Mean	Lin	-	55	12	-14.92	0.04	41	-	54	17	-39.08	7.5 e-05	1
2	Temperature	Max	Lin	-	52	14	-14.29	0.13	49	-	28	28	-22.46	7.6 e-05	10
3	Temperature	Min	Lin	-	310	310	-8.99	0.75	90	-	28	28	-22.46	0.1	56
4	Temperature	Mean	Quad	-	236	234	-12.77	0.84	52	-	17	54	-37.72	0.001	1
5	Temperature	Max	Quad	-	32	14	-15.01	0.32	52	-	28	28	-20.10	0.05	20
6	Temperature	Min	Quad	-	308	299	-11.37	0.84	73	-	28	28	-20.10	0.12	37
7	Rain	Mean	Lin	-	27	22	-11.35	0.73	92	-	74	8	-18.05	6.2 e-05	6
8	Rain	Max	Lin	-	24	22	-14.54	0.78	91	-	64	6	-8.66	0.88	84
9	Rain	Min	Lin	-	175	174	-5.92	0.74	94	-	111	107	-10.18	0.94	94
10	Rain	Mean	Quad	-	24	17	-15.46	0.87	62	-	24	38	-19.21	0.001	7
11	Rain	Max	Quad	-	24	19	-17.33	0.24	42	-	250	250	-8.32	0.99	67
12	Rain	Min	Quad	-	330	330	-5.07	0.74	94	-	64	6	-11.20	0.94	94
ECE	Temperature	Sum	Lin	17.15	47	24	-18.24	0.002	5	18.15	50	17	-17.78	0.002	32
Cue 1 + ECE	Temperature	Sum	Lin	17.15	47	24	-25.84	0.21	62	18.15	50	33	-49.10	0.03	50
						.									
	Parameters			D-Muro		Cate	rpillars			E-Pirio					
Model	Cue	Statistic	Function	Threshold	Open	Close	ΔAIC	Pc	%CI	Threshold	Open	Close	ΔAIC	Pc	%CI
1	Temperature	Mean	Lin	-	88	33	-21.17	0.001	7	-	94	8	-24.8	0.0002	2
ECE	Temperature	Mean	Lin	15.92	88	57	-15.91	0.005	21	21.7	41	40	-9.26	0.25	64
Cue 1 + ECE	Temperature	Mean	Lin	15.92	78	76	-10.73	0.14	60	21.7	18	18	-6.45	0.74	82

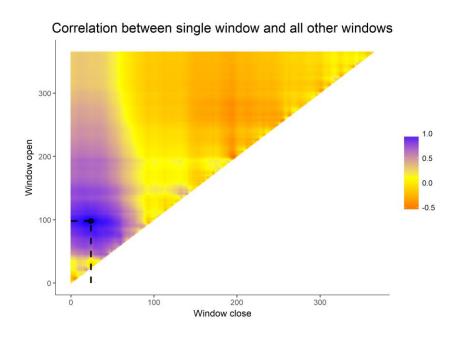
Estimated best and median mean temperature cue windows (see electronic supplementary material Box S2 for details about choice of best windows and estimation of median windows). $1 = 1^{st}$ January. Negative value of ordinal means day in the previous year (before 1^{st} January).

		Blue	e tits		Caterpillars				
<u>Ordinal day</u>	Best Wind	wob	Median window		Best Window		Median window		
(1= 1 st January)	Open	Close	Open	Close	Open	Close	Open	Close	
<u></u>	day	day	day	day	day	day	day	day	
D-Rouvière	17	91	22	91	-	-	-	-	
D-Muro	35	97	19	88	42	97	10	107	
E-Muro	74	117	-75	89	-	-	-	-	
E-Pirio	90	127	87	130	72	158	80	156	

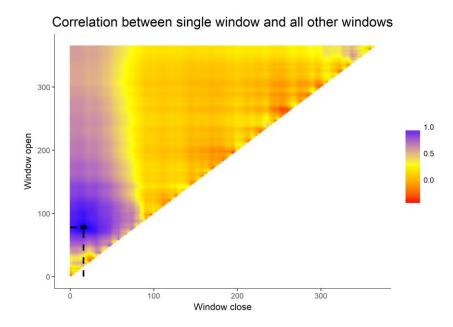
Figure S2

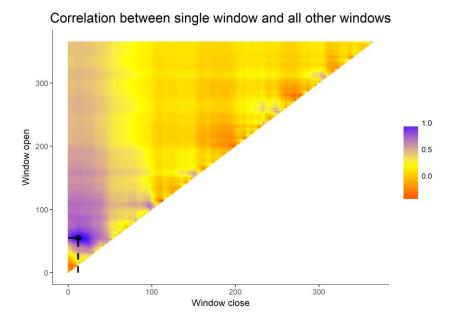
Correlation between the window estimated from the best model (represented by the black dot) and all other possible windows of mean temperature for a) D-Rouvière, b) D-Muro, c) E-Muro and d) E-Pirio population (positive autocorrelation in purple; negative autocorrelation in red). Graphics from the function autowin in climwin R package. Some differences in patterns of correlation are visible among populations: in deciduous populations, the peak of correlation is less steep than in the evergreen populations. This is in line with the interpretation that the environment is less predictable in evergreen populations.

a)

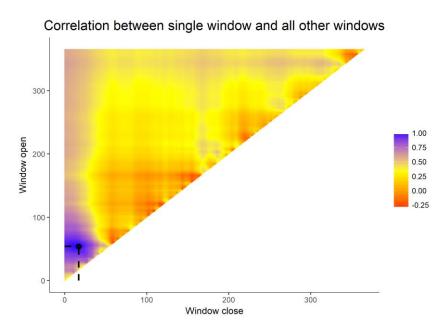


b)





d)



c)

Temporal trend in the number of positive ECE at 5% during the cue window. r^2 is the coefficient of determination. Significant slopes (p-value < 0.05) are in bold. Sample sizes are given in Table S1.

Number of ECE	t-value	p-value	r ²
(per decade, ± se)			
0.73 (± 0.71)	1.03	0.31	0.002
0.71 (± 0.29)	2.45	0.02	0.11
0.49 (± 0.16)	2.98	0.005	0.16
1.8 (± 0.5)	3.48	0.001	0.21
	5	(per decade, ± se)0.73 (± 0.71)1.030.71 (± 0.29)2.450.49 (± 0.16)2.98	(per decade, ± se)0.73 (± 0.71)1.030.310.71 (± 0.29)2.450.020.49 (± 0.16)2.980.005

Blue tit reaction norm favoured by selection estimated by the regression of the date of caterpillar peak abundance on the detected cues for blue tits. For evergreen populations, we present results for cues taken both as mean temperature (MeanT) and the number of positive ECEs. Models with both MeanT and ECE are not better than models with MeanT (or ECE) alone (not shown). r^2 is the coefficient of determination. Significant slopes (p-value < 0.05) are in bold. Sample sizes are given in Table S1.

	Climate	Intercept				r ²		
		Estimates (± se)	t-value	p-value	Estimates (± se)	t-value	p-value	
D-Rouvière	MeanT	192.72 (± 29.17)	6.61	0.0002	-8.39 (± 3.62)	-2.32	0.049	0.33
D-Muro	MeanT	169.02 (± 9.02)	18.75	<0.0001	-4.88 (± 0.83)	-5.90	<0.0001	0.59
E-Muro	MeanT	228.36 (± 39.36)	5.80	<0.0001	-7.99 (± 2.93)	-2.73	0.02	0.29
L-IVIUIO	ECE	125.42 (± 3.94)	31.81	<0.0001	-1.87 (± 1.50)	-1.25	0.23	0.03
E-Pirio	MeanT	216.74 (± 20.87)	10.39	<0.0001	-4.43 (± 1.47)	-3.01	0.005	0.21
	ECE	162.07 (± 2.38)	68.09	<0.0001	-0.97 (± 0.25)	-3.84	0.0006	0.31

Synchrony between blue tits and their preys, assessed by the regression between mean laying date of blue tits and caterpillar date of peak abundance. r^2 is the coefficient of determination. Significant slopes (p-value < 0.05) are in bold. Sample sizes are given in Table S1.

	Ir	ntercept			r²		
	Estimates (± se)	t-value	p-value	Estimates (± se)	t-value	p-value	
D-Rouvière	8.33 (± 76.56)	0.11	0.92	1.21 (± 0.79)	1.53	0.16	0.13
D-Muro	7.50 (± 14.85)	0.51	0.62	1.11 (± 0.15)	7.32	<0.0001	0.69
E-Muro	8.40 (± 46.03)	0.18	0.86	1.06 (± 0.43)	2.45	0.03	0.24
E-Pirio	44.74 (± 24.38)	1.83	0.08	0.85 (± 0.19)	4.49	0.0001	0.39

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