

1 **Supplementary material**

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3 **Habitat choice meets thermal specialization: competition with specialists may drive**
4 **suboptimal habitat preferences in generalists**

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26 ***Quantification of habitat choice in *Tetrahymena thermophila* microcosms***

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28 To quantify the relationship between dispersal decisions and expected fitness, and thus the
29 habitat choice strategies of genotypes, we fitted a simple model in which dispersal rates (D_e
30 for emigration; see below for immigration) depend on expected fitness \bar{f} , habitat choice (h_e
31 for emigration; h_i for immigration; see below) and dispersal propensity (Dp_e ; the tendency to
32 disperse at $\bar{f} = 0.5$) using the functions:

$$D_e = Dp_e - h_e (\bar{f} - 0.5)$$

33 At the emigration step, we fitted the above model using the *nls* function from the *stats* R-
34 package, with 10 values of D_e for each genotype corresponding to emigration rates in the 10
35 dispersal systems used. The input variables of the model were \bar{f} and D_e , while h_e and Dp_e
36 were estimated using the *nls* function, as well as the variance of these estimates (Figure 3;
37 Table S2). To avoid dispersal rate values outside the [0,1] limits when $Dp_e \neq 0.5$, we
38 constrained habitat choice values within $[-2 \min(Dp_e, 1-Dp_e), +2 \min(Dp_e, 1-Dp_e)]$ using the
39 *nls* function. This assumes that habitat choice ability decreases when dispersal propensity
40 deviates from 0.5, meaning, for instance, that a genotype with a low dispersal propensity will
41 never reach a probability = 1 to leave a suboptimal habitat. We also estimated habitat choice
42 using a model that does not make this assumption, but consequently assumes a nonlinear
43 relationship between habitat choice h and expected fitness \bar{f} , and habitat choice estimates
44 were highly correlated between these two methods ($R^2 = 0.971$).

45 At the immigration step, two immigration rates were quantified for each 3-patch dispersal
46 system: the proportion of dispersers that moved toward the 27°C patch and the proportion that
47 moved toward the 35°C patch. This resulted in 10 pairs of immigration rates D_i for each
48 genotype. Because these two proportions are dependent (their sum is equal to one), we

49 subtracted the following habitat choice equations (i.e. one for immigration toward 27°C and
50 one toward 35°C)

$$D_{i\ 27^{\circ}C} = Dp_i + h_i (\bar{f}_{27^{\circ}C} - 0.5)$$

51 and

$$D_{i\ 35^{\circ}C} = Dp_i + h_i (\bar{f}_{35^{\circ}C} - 0.5)$$

52 leading to

$$D_{i\ 27^{\circ}C} - D_{i\ 35^{\circ}C} = h_i (\bar{f}_{27^{\circ}C} - \bar{f}_{35^{\circ}C})$$

53 This resulted in 10 independent estimates of habitat choice at immigration (i.e. one for
54 each 3-patch system):

$$h_i = \frac{D_{i\ 27^{\circ}C} - D_{i\ 35^{\circ}C}}{\bar{f}_{27^{\circ}C} - \bar{f}_{35^{\circ}C}}$$

55 We used the mean of these 10 values as the final estimate of habitat choice h_i for each
56 genotype. Note that subtracting the habitat choice equations at immigration allows removing
57 the parameter Dp_i from the resulting equation, with estimated dispersal propensity being the
58 tendency of a genotype to emigrate (i.e. Dp_e). The expected fitness \bar{f} in the start patch was
59 used for habitat choice at emigration and expected fitness in neighbouring patches was used
60 for immigration, with habitat choice estimated separately for emigration and immigration.

61 Quantifying habitat choice using the above-described model allows quantifying
62 standardized habitat choice parameters within the [-1,1] limits. The resulting estimates are
63 equal to regression estimates, except in some cases when low expected fitness differences
64 between temperatures coupled with important emigration or immigration ratio make simple
65 regression estimates to go out the [-1,1] limits (Pearson correlation between standardized
66 habitat choice values and regression estimates at emigration: 1; $t_{10} = \text{Inf}$; $p < 0.001$; at
67 immigration: 0.84; $t_{10} = 4.98$; $p < 0.001$).

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69 ***Construction of thermal niches in the model***

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71 In the metapopulation model, the spatiotemporal variability is such that local temperature
72 varies between a cold T_1 , a central T_2 and a warm temperature T_3 . Hence we constructed the
73 thermal niches based on thermal optimum and degree of specialization to define three fitness
74 values $f_i(T_1)$, $f_i(T_2)$ and $f_i(T_3)$ for each strategy i . The thermal optimum is the temperature at
75 which fitness is maximal (either T_1 , T_2 or T_3), and the degree of specialization determines the
76 fitness difference between the optimal habitat and the other temperatures (the larger this
77 difference, the more specialist the strategy).

78 We imposed a specialist-generalist trade-off between the three fitness values of the thermal
79 niches, with α denoting the strength of the trade-off:

$$f_i(T_1)^{\frac{1}{\alpha}} + f_i(T_2)^{\frac{1}{\alpha}} + f_i(T_3)^{\frac{1}{\alpha}} = 1$$

80 Each strategy i is defined by a degree of specialization s_i , taking values between 0 (for the
81 perfect generalist) and 1 (for a perfect specialist), given by:

$$s_i = \frac{\max \{ f_i(T_1), f_i(T_2), f_i(T_3) \} - \frac{1}{3^\alpha}}{1 - \frac{1}{3^\alpha}}$$

82 A perfect specialist has one fitness value equal to 1 and the two others equal to 0, while the
83 perfect generalist has three identical fitness values $f_i(T_1) = f_i(T_2) = f_i(T_3) = \frac{1}{3^\alpha}$. We imposed
84 symmetric thermal niches when the thermal optimum is the central temperature T_2 (see
85 second row in Figure S3). For specialists of the cold and warm margins, we assumed a linear
86 decrease of fitness when moving away from the optimum (see for instance top right niche in
87 Figure S3, with the fitness at the central temperature T_2 set to the mean of the fitness values at
88 the margins: $f_i(T_2) = \frac{1}{2} (f_i(T_1) + f_i(T_3))$). For the most specialist strategies in which a
89 linear decrease of fitness would lead to negative fitness values at the second margin (i.e. when

90 $f_i(T_1) > (1 + 2^{-\frac{1}{\alpha}})^{-\alpha}$, we set the fitness at the second margin to 0 (see for instance top left
91 in Figure S3).

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93 To construct the pool of competing strategies, we first selected a set of thermal niches. We
94 varied the degree of specialization from 0 to 1 in 20 steps, and this for the three possible
95 thermal optima (see Figure S3). Together with the perfect generalist, this led to 61 thermal
96 niches. Each of these thermal niches was then combined with habitat choice parameter h_i
97 varying from -1 to 1 in steps of 0.2 . This resulted in a pool of $61 \times 11 = 671$ competing
98 strategies. We verified that qualitatively similar results were obtained for other choices of the
99 strategy pool.

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101 **Table S1:** List of the genotypes used in this study. Identities of genotypes (code) and
 102 identifying numbers at the Tetrahymena Stock Centre, Cornell (TSC ID) are shown.

Code	TSC ID	Sampling done by	City	isolation date	reference
D1	SD01546	Doerder FP	Ridgway	21/08/02	Zufall et al. 2013. Mol.Ecol
D2	SD01547	Doerder FP	Ridgway	21/08/02	Zufall et al. 2013. Mol.Ecol
D3	SD01548	Doerder FP	Warren	01/06/03	Zufall et al. 2013. Mol.Ecol
D4	SD01549	Doerder FP	Warren	01/06/03	Zufall et al. 2013. Mol.Ecol
D6	SD01551	Doerder FP	Warren	01/06/03	Zufall et al. 2013. Mol.Ecol
D7	AK III	Doerder FP	unknown	unknown	Zufall et al. 2013. Mol.Ecol
D8	SD01553	Doerder FP	Owl's Nest	30/07/08	Zufall et al. 2013. Mol.Ecol
D10	SD01557	Doerder FP	Alstead	22/07/09	Zufall et al. 2013. Mol.Ecol
D11	SD01558	Doerder FP	Washington	24/07/09	Zufall et al. 2013. Mol.Ecol
D12	SD01556	Doerder FP	Guys Mills	26/08/08	Zufall et al. 2013. Mol.Ecol
D13	SD01555	Doerder FP	Guys Mills	26/08/08	Zufall et al. 2013. Mol.Ecol
D17	SD01561	Doerder FP	Antrim	24/07/09	Zufall et al. 2013. Mol.Ecol

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107 **Table S2:** Estimates of habitat choice for each genotype at emigration and immigration. *t*-
 108 statistics compared to 0 are shown, with n=10 replicates for each genotype.

strains	Habitat choice at emigration				Habitat choice at immigration			
	h_e	sd	<i>t</i>	p	h_i	sd	<i>t</i>	p
D1	0.494	0.531	2.94	0.016	0.110	0.945	0.519	0.617
D2	-0.459	0.211	-6.87	<0.001	-0.933	0.154	-27.086	0.000
D3	-0.278	0.274	-3.20	0.011	-0.312	0.596	-2.338	0.044
D4	0.366	0.153	7.58	<0.001	0.111	0.793	0.629	0.545
D6	-0.334	0.171	-6.18	<0.001	-0.574	0.401	-6.398	<0.001
D7	0.143	0.431	1.05	0.323	0.953	0.1450	29.382	<0.001
D8	-0.325	0.188	-5.46	<0.001	0.749	0.496	6.757	<0.001
D10	-0.246	0.282	-2.75	0.022	-0.809	0.349	-10.364	<0.001
D11	0.435	0.105	13.15	<0.001	0.690	0.313	9.864	<0.001
D12	-0.368	0.331	-3.51	0.007	-0.519	0.736	-3.153	0.012
D13	0.599	0.119	15.86	<0.001	-0.008	0.827	-0.041	0.968
D17	0.579	0.108	17.03	<0.001	0.053	0.615	0.383	0.711

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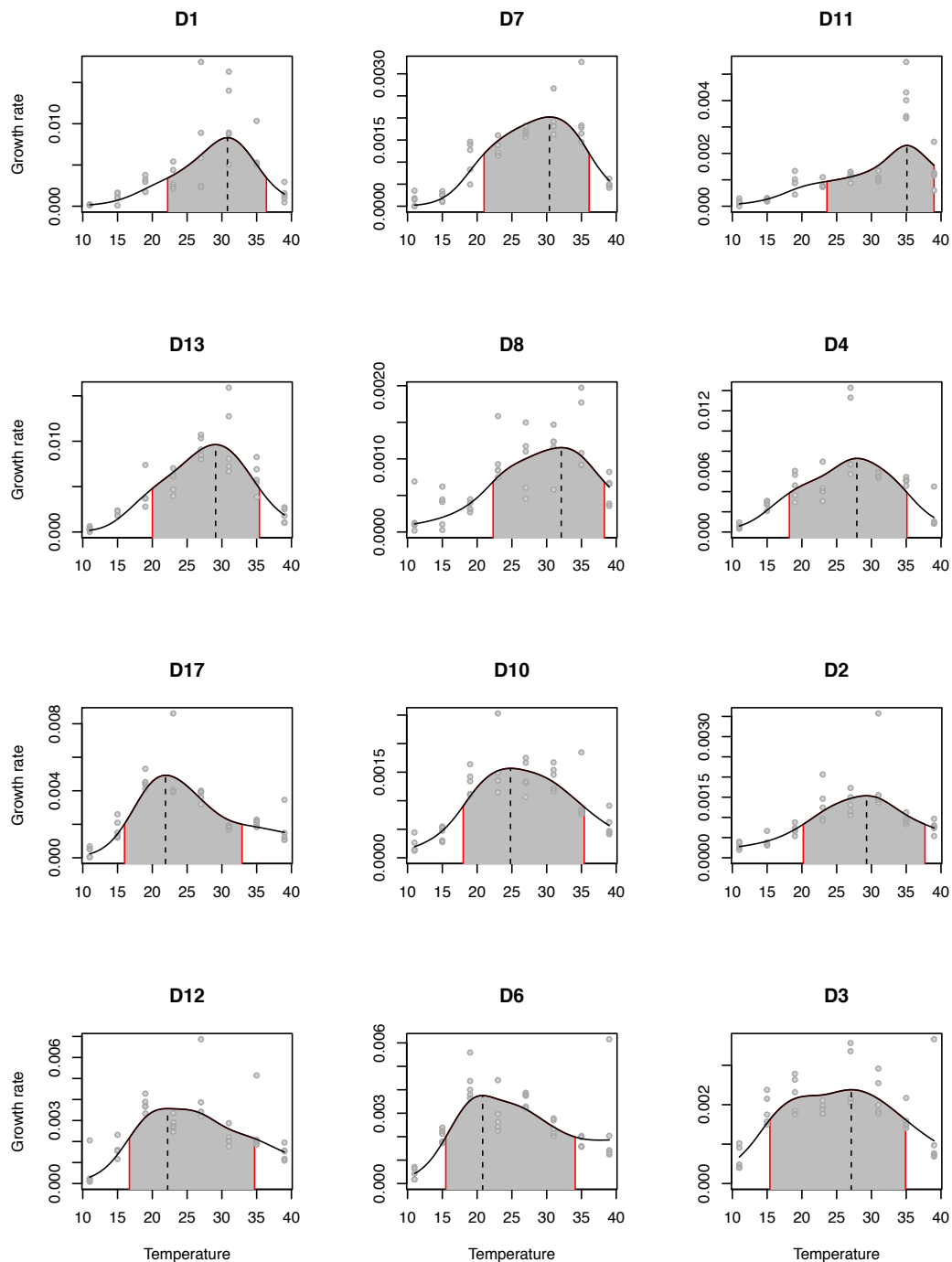
111 **Table S3:** Variance partitioning analysis showing the contribution of niche width to the
 112 variance in habitat choice at emigration and immigration. The unique contributions, that is the
 113 percentage of variance explained, of niche width are higher than unique contributions of
 114 thermal optimum in both cases. Interestingly, thermal optimum also explains variability in
 115 habitat choice at immigration.

<u><i>Habitat choice h_e</i></u> <u><i>at emigration</i></u>	<u>Unique</u>	<u>Common</u>	<u>Total</u>
Niche width	0.411	0.034	0.445
Thermal optimum	0.045	0.034	0.079
<u><i>Habitat choice h_i</i></u> <u><i>at immigration</i></u>	<u>Unique</u>	<u>Common</u>	<u>Total</u>
Niche width	0.115	0.333	0.448
Thermal optimum	0.061	0.333	0.394

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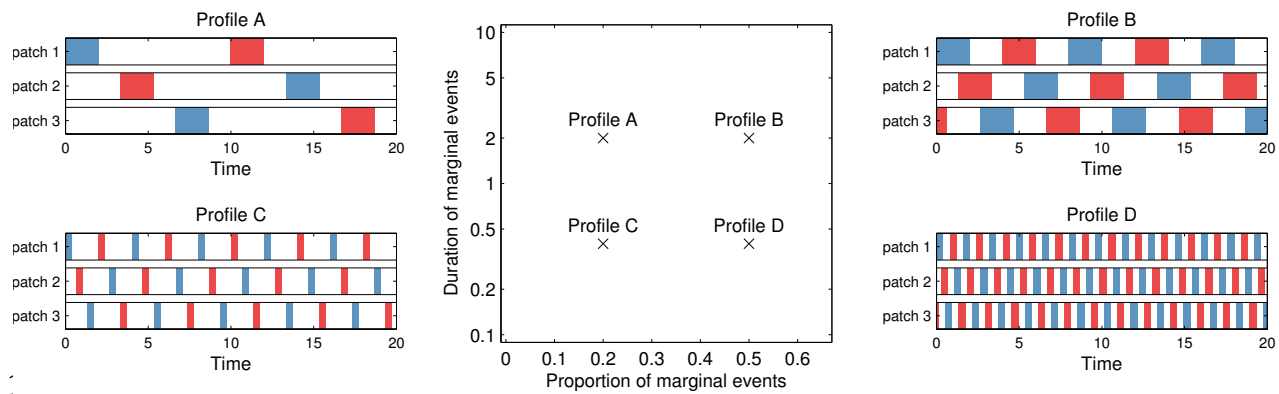
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118 **Figure S1:** Thermal niches of *T. thermophila* genotypes, sorted from the most specialist (top-
119 left) to the most generalist (down-right). Points represent growth rate of each replicate along
120 the thermal gradient (four replicates per temperature for each genotype). The black line
121 corresponds to the fit of a general additive model of growth rate as a function of temperature.
122 The grey area represents *niche width* (the temperature range containing 80% of the thermal
123 niche), and the dashed line shows *thermal optimum*.



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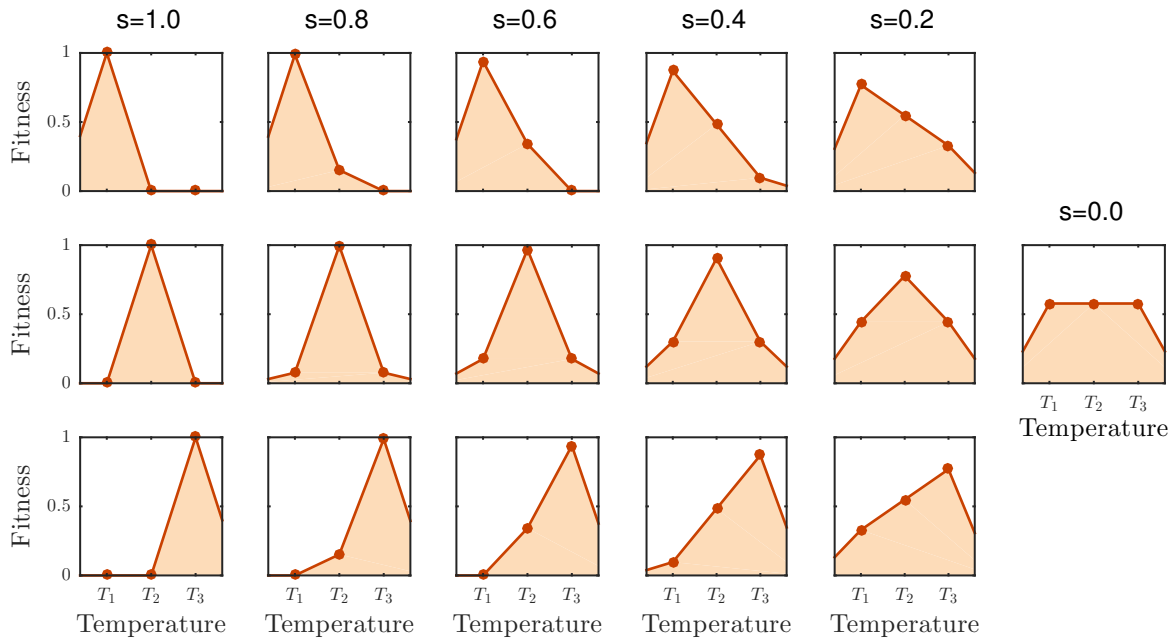
125 **Figure S2:** Illustration of the spatiotemporal variability of environmental conditions in the
 126 model. The temperature variability profiles consist in periods of the central temperature T_2
 127 (white) intertwined with periods of a marginal temperature T_1 (blue) or T_3 (red). Each
 128 temperature variability profile is characterized by two parameters: the proportion of time
 129 during which the temperature is marginal p_m (x-axis in the central panel) and the duration of
 130 each period of marginal conditions t_m (y-axis in the central panel). Profiles A to D illustrate
 131 four scenarios of spatiotemporal variability in the 3-patch metapopulations, with the
 132 respective combinations of p_m and t_m indicated in the central panel.



134

135 **Figure S3:** Illustration of thermal niches used in the simulations, defined based on thermal
 136 optimum and degree of specialization to define three fitness values $f_i(T_1)$, $f_i(T_2)$ and $f_i(T_3)$ for
 137 each strategy i , and satisfying the specialist-generalist trade-off. The figure shows 16 thermal
 138 niches, differing in their thermal optimum (different rows) and their degree of specialization s_i
 139 (different columns). Note that in the simulations we used a larger set of 61 thermal niches,
 140 each combined with an habitat choice value between -1 and 1, resulting in a total of $61 \times 11 =$
 141 671 competing strategies.

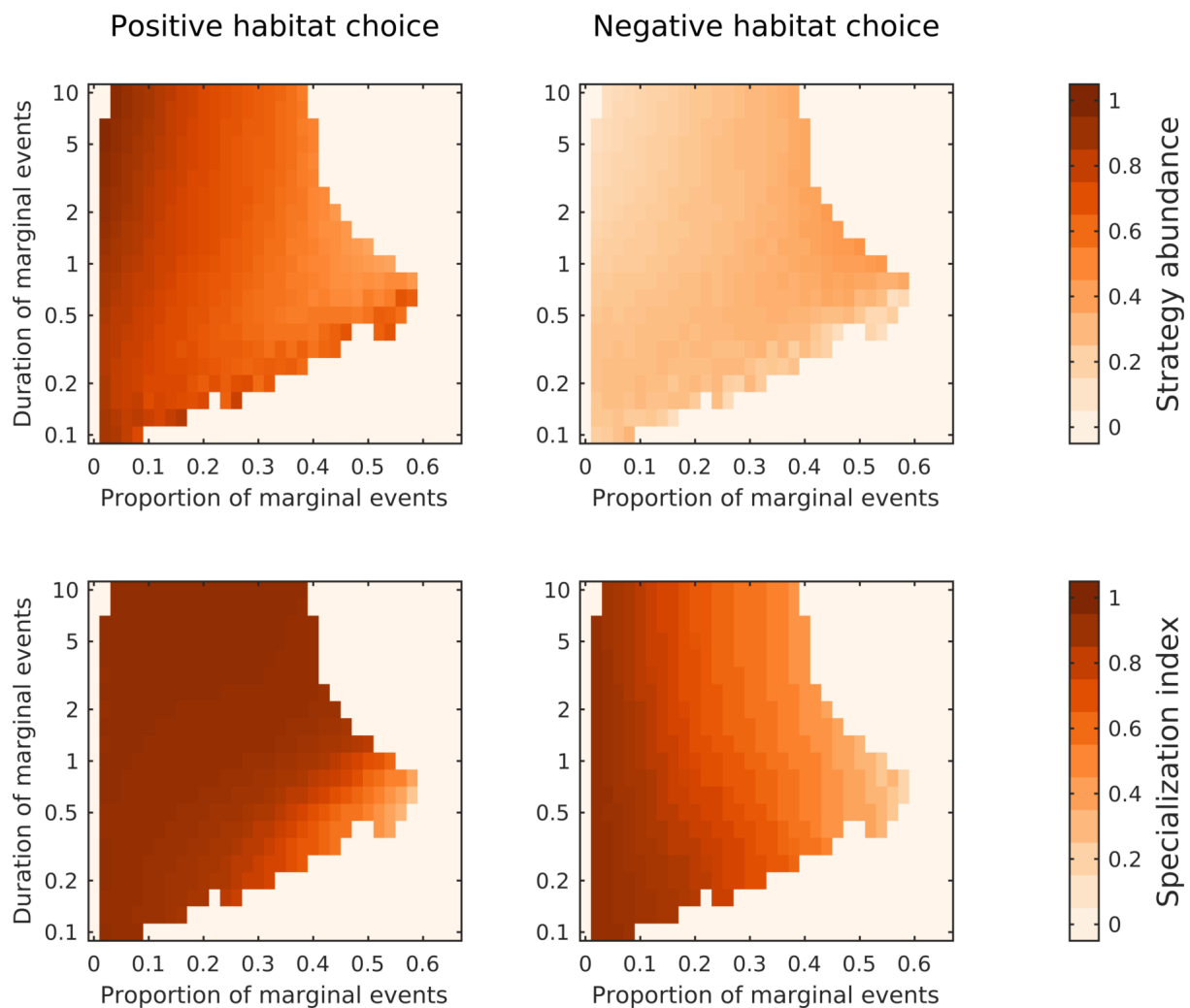
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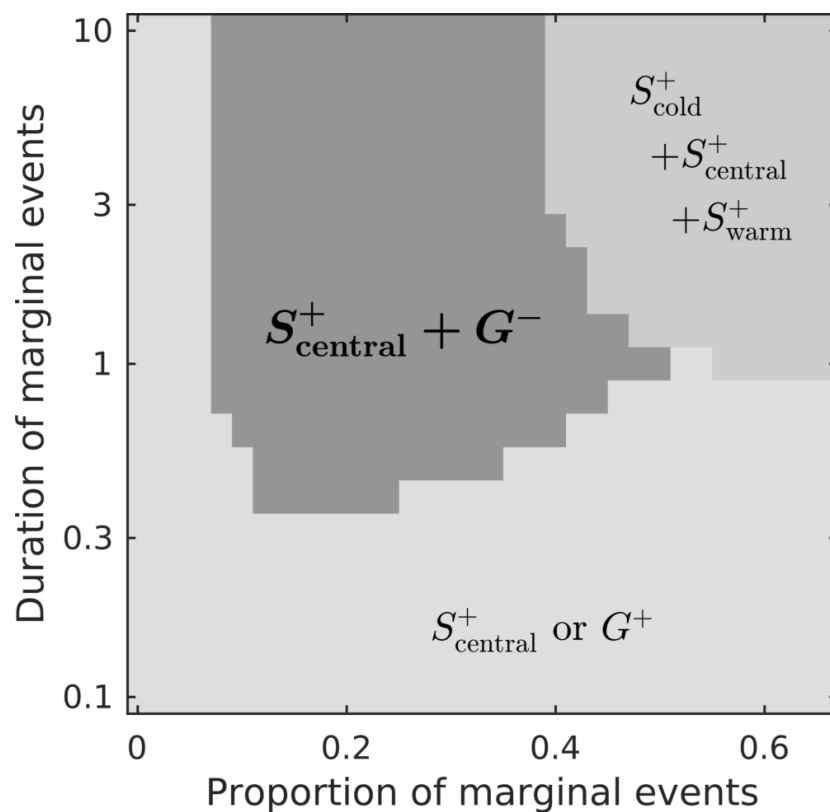
145 **Figure S4:** Abundance and degree of specialization of the two strategies coexisting in the
 146 region labelled $S_{central}^+ + G^-$ in Fig. 4 (with positive and negative habitat choice,
 147 respectively). Left: specialist with positive habitat choice. Right: generalist with negative
 148 habitat choice. Top panels: abundance, averaged over time and expressed as fraction of
 149 carrying capacity. The generalist strategy with negative habitat choice represents about 20%
 150 of the total metapopulation abundance. Bottom panels: specialization, a number between 0
 151 (perfect generalist) and 1 (perfect specialist). The strategy with negative habitat choice,
 152 meaning that it moves preferentially to the niche margins, show specialization index close to
 153 one when the proportion of marginal events is small (but still remains more generalist than the
 154 strategy with positive habitat choice).



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157 **Figure S5** : The coexistence of generalists with a preference for suboptimal habitats and
 158 specialists with a preference for optimal habitats is robust with respect to model assumptions.
 159 The figure is similar to Figure 4, but here we extend the model with the following features:
 160 (1) a dispersal cost: we assume that 5% of the emigrants die before settling in their
 161 destination patch; (2) a habitat choice cost: we assume that a strategy with habitat choice
 162 parameter h has a fitness reduction of $0.01 |h|$ compared to a strategy without habitat choice
 163 ($h=0$); (3) smaller competition between than within strategies: we assume that the strength of
 164 competition between individuals with different strategies equals 90% of the strength of
 165 competition between individuals with the same strategy. Due to these model modifications,
 166 the region in which a generalist with negative habitat choice ($h<0$) persists shrinks, but still
 167 covers an important part of the parameter space (dark grey region, compare with Fig. 4).



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