

Temperature niche difference and interspecific competition determine the parapatric distribution of two congeneric species in *Diaphanosoma*

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Abstract

Background *Diaphanosoma excisum* and *D. dubium* are parapatrically distributed in tropical and subtropical waters, and rarely coexist at local communities in the transition between tropics and subtropics. According to Janzen's hypothesis and the modern coexistence theory, the specific thermal adaptation and strong interspecific competition between the two congeneric species are assumed to result in their range limits. To explore the mechanisms underlying such parapatric distribution, we modeled their current geographic distribution, and compared temperature niche difference and fitness inequality in interspecific competition with their representative clones.

Results The species distribution modeling showed that the two *Diaphanosoma* species had significantly divergent climate niches. Their life history parameters in monocultures also demonstrated as stable temperature niche difference, while *D. excisum* had higher fitness than *D. dubium* in dimension of food niche. The competition experiments revealed a strong exploitative competition between the two species, and *D. excisum* was the superior competitor, and excluded *D. dubium* in all the competition experiments within overlapping temperature niche regardless of food conditions.

Conclusions Our results suggest that stable temperature niche difference overcoming interspecific competition for food plays a critical role in shaping *Diaphanosoma* species range.

Background

The primary goal of ecology and biogeography is to understand the spatial distribution of species [1–4]. Species range largely depends on their niche: an n-dimensional hypervolume defined by axes of environmental conditions and resource use within which populations of a species are able to maintain a positive intrinsic rate of increase [5–7]. Temperature affects most key life history traits and has long been recognized as the most fundamental dimension of niche space, which determines species geographical distribution [8, 9]. Change in temperature will significantly affect species adaptation and spatial distribution [10–12]. In tropics, species experience a rather stable thermal condition, and consequently, they are predicted to have narrower temperature niches than their counterparts from higher latitudes and become more sensitive to temperature variation [10, 13]. In high latitudes, where annual temperature largely fluctuates, species have broad temperature tolerance threshold. Food availability is another fundamental niche dimension, which determines species food utilization rate and realized fitness [14]. Individuals of one species that use marginal resources do not exploit resources as efficiently as those for which these resources are nearly optimal [14].

In the modern coexistence theory, species coexistence requires stable niche difference or fitness equality [15–17]. Congeneric species are considered to be more similar in niche space than species from different genera, resulting in strong competition in overlapping habitats [4, 18, 19]. *Diaphanosoma* is a high diversity genus of Cladocera, commonly dominating in tropical and subtropical freshwaters. Two congeneric species, *D. dubium* and *D. excisum* are common in tropics or subtropics but rarely coexist at

local communities [20–22]. In tropics, *D. excisum* is frequently present as the only representative of Cladocera [23]. *D. dubium* is widespread in subtropical China while *D. excisum* is restricted to the coastal islands of the southern China [24]. The mean temperature of the coldest month (January) at the northern limit of the distribution of *D. excisum* in this region is about 15 °C, while the northward limits of *D. dubium* reaches the lower Amur river [21]. Pajk et al. [25] measured the life history traits of clones from 16 populations of *D. dubium* and *D. excisum* under a large temperature range from 10 °C to 40 °C, and showed the tropical *D. excisum* had narrower thermal performance curves (TPCs) and higher optimum temperature than the subtropical *D. dubium*, but failed to reproduce at ≤ 15 °C. The authors concluded that negative r below 15 °C in combination with competition from the cold-adapted *D. dubium* limited northward distribution of *D. excisum*. Due to the similarity in body size and feeding by filtration of shared prey - small phytoplankton and bacteria, strong exploitative competition between the two congeneric species is expected when total abundance approaches the carrying capacity, and strong interspecific competition may constraint the southward distribution of the cold-adapted *D. dubium* in China. However, the temperature niche and the competition for food between the two species in temperatures above 15 °C remain unclear.

To illustrate the temperature niche difference, we first calculated climate niche overlap between the two congeneric species under a species distribution model. To check further temperature niche and interspecific competition between *D. dubium* and *D. excisum*, we compared the thermal performance curve and conducted competition experiments at combinations of two temperature and two food concentrations.

Methods

Species distribution modeling

Species data were simple presence observations based on records from checklist and our field sampling. Occurrence records for *D. dubium* were mostly referred to [22], our consecutive sampling as well as field observation. Occurrence records for *D. excisum* were mostly from the published literature. *D. excisum* was widely distributed in tropics and subtropics of Australia, Asia and Africa, up to eastern China. No records were reported for both species from South America, North America and Antarctic. In total, 165 populations for *D. dubium* and 162 populations for *D. excisum* were used for species distribution models (see Additional file 1).

We used a comprehensive set of 19 bioclimatic variables with a spatial resolution of 2.5 arc min (about 4 km in the study area) as climate predictors available through <http://www.worldclim.org> [26]. We computed pair-wise spearman rank correlations to assess multi-collinearity of the 19 worldclim variables, wherein species distribution models (SDMs) were developed with a subset of variables with $R^2 < 0.75$: bio2, bio3, bio5, bio6, bio8, bio13, bio14, bio15, bio18, bio19 (see Additional file 1). For each species we use the modelled association between current climate and present-day distribution to estimate current distributional areas.

We performed spatial predictions of the two species distributions in 'ecospat' written in R language [27], which provided methods and utilities for quantifying climatic niches shifts between two congeneric peripheral distribution species, analyzing niche overlap between them [28]. We used a shape file containing presence-absence records for a species as spatial points generated in QGIS v2.18. Raster datasets (in grid format) of above ten worldclim variables were used as explanatory variables (predictors). Coupled with selected explanatory variables, the shape files with only occurrence data of both *D. excisum* and *D. dubium* were used to perform modeling and evaluation with package 'sdm'. Four models ('rf' (Random Forest), 'brt' (Generalized Boosting Model or usually called Boosted Regression Trees (gbm)), 'bioclim' (Surface Range Envelop (sre), 'glm' (Generalized Linear Model)) were used for model training. Roc curves were used to compare the results for all models. Then we just predicted the habitat suitability into the whole study area, and fitted habitat suitability value of each present-absent site for each model were obtained from the output shapefiles in QGIS v2.18 (see Additional file 1).

For pre-modeling, we investigated spatial autocorrelation of climate predictors by Mantel correlogram to determine the minimal distance between species records. We performed Niche quantification and comparison with ordination techniques. The PCA was calibrated on all the sites of the study area to describe the contribution of all original predictors, covering the ranges of the two study species [29]. Niche overlap in terms of Schoener's D was computed based on kernel density estimates for both species occurrence records in PCA space accounting at the same time for the relative frequency of specific climate conditions within the study area. The results allowed a quantification of those parts of niche space occupied by both species as well as the unique parts of two species. The classification of Schoener's D was proposed by Rödder and Engler [30].

Randomization tests for niche equivalency and similarity as proposed by Warren et al. [31] were computed to test the hypothesis of niche equivalency and niche similarity [32]. Parameter alternative was set as 'greater' to test for niche conservatism, i.e. whether the overlap is more equivalent/similar than random. For Core Niche Modeling, we accessed the calibration capacity of our models using a repeated split-plot approach [33]. We used a random subsample of 75% of the points of presence to calibrate the models using the approach described above, and the remnant 25% to evaluate the model, repeating the whole procedure 10 times. Presence-only data were used to calculate the Boyce Index for each model [34], as Boyce index measured how much model predictions differ from a random distribution of the observed presences across the prediction gradients [35]. Finally, we ensemble selected small models with the Boyce index more than 0.80 for spatial predictions with current climatic variables. Once the models were calibrated and evaluated, we projected the potential distribution of the species over space. Spatial projections were visualized and plotted in QGIS v2.18. All statistical analyses were performed using R 3.5.3 [27], and the packages being "biomod2", "ecospat", "sdm", "maptools", "raster", "rgdal", "rtiff".

Life history and temperature niche

Analysis of temperature niche difference between the two species was conducted with two representative clones, one for *D. dubium* and another for *D. excisum*. *D. dubium* (clone N) was collected from a fish pond on the way to Changtang reservoir, Shaoguan, China (N24°78', E113°50'). *D. excisum* (clone D) was collected from Hedi reservoir, Zhanjiang, China (N21°85', E110°31'). The two clones chosen were each the best performing clone of its species from our previous life history experiments with 16 *Diaphanosoma* clones [25]. We measured their life history traits (net reproductive rate (R_0), intrinsic rate of population increase (r)) under a temperature range from 10°C to 40°C. 40°C was estimated to be above the critical thermal maximum (CT_{max}), while 10°C was estimated to be below the critical thermal minimum (CT_{min}) [25]. Life table experiments were conducted at 15, 20, 25, 30, 34, and 38 °C. There were at least five replicates per clone by temperature combination; replicates being single individuals in 30 mL of medium. Additional replicates were added in environments with high juvenile mortality ($T > 34^\circ\text{C}$). The detailed life history experiments and parameter calculation were described in Pajk et al. [25]. As temperature curve performance of R_0 and r can be used as representative of temperature niche, they were fitted by mixed linear models with the *lme* function from the R package “nlme” [36]. The choice of the best fit was made through comparison of the AICc.

Interspecific competition experiments

The competition experiments were conducted with above clones of two species of *Diaphanosoma*. The 12±12 h old second clutch offspring of the F_3 -generation were used to start the experiments. The experiments were run at two temperatures (20°C and 30°C) and food levels (1.0 mgC/L and 0.5 mgC/L) [37]. The temperatures chosen are representative of the localities of *D. dubium* and *D. excisum*, while the food levels are selected from the life history experiments of *D. dubium* and *D. excisum*, in which a sound intrinsic rate of increase ($r > 0.2$) was obtained at above 0.5 mgC/L.

Animals were kept in 300 mL of medium. Monoculture replicates initially contained 10 neonates of a single species. Competition replicates were started with 10 neonates of each species. The number of animals in each treatment was recorded every six days at 20°C and every four days at 30°C. For each replicate we determined the maximum density and the maximum growth rate

$$(r_{max} = \max(\ln N_t - \ln N_0)/t, \dots)$$

N_0 and N_t : population densities at two consecutive samplings). We calculated r of the two species in both competition cultures and monocultures [38-40]. These parameters were compared between the treatment groups (species×T×food×monoculture/competition culture) with a factorial ANOVA (SPSS 16.0).

Results

Species distribution and climate niche overlap

Climate niche overlap between *D. dubium* and *D. excisum* was low (Schoener's D = 0.218) (Fig. 1c). The climatic predictors of Mean Diurnal Range, Min Temperature of Coldest Month, Precipitation of Driest month, Precipitation of warmest Quarter, and Precipitation Seasonality contributed more than the rest variables (see Additional file 2). With a value of $p=1/p=0.73$, we accepted the hypothesis that the niche overlap between sister species *D. dubium* and *D. excisum* (see Additional file 3) is more equivalency /similarity than random.

For four tested models, the Boyce indexes were all listed in Table 1. The rank of predicted expected ratio ordered along habitat suitability axis was plotted (see Additional file 4). Model 'glm' had the best calibration capacity for the dataset (*D. dubium*: Boyce index=0.926; *D. excisum*: Boyce index=0.906), followed by model 'rf' (*D. dubium*: Boyce index=0.883; *D. excisum*: Boyce index=0.805). Based on Boyce index, both 'glm' and 'rf' were used for species distribution projection. We generated a species distribution model as well as climate niche overlap analysis for both *D. dubium* and *D. excisum* populations (Fig. 1a, b). The results demonstrated a strong niche separation of the two *Diaphanosoma* species.

Life history and temperature niche

D. dubium had a broad temperature niche and was able to reproduce at $<20^{\circ}\text{C}$ (Fig. 1d, e). *D. excisum* had a narrower temperature niche and failed to reproduce at $<20^{\circ}\text{C}$, but higher net reproductive rate (R_0) and fitness (r) than *D. dubium* at $\geq 20^{\circ}\text{C}$ (Fig. 1d, e).

Fitness inequality and interspecific competition

Temperature, food level and competition all had a significant effect on maximum density (Table 2). *D. excisum* had higher average maximum population density than *D. dubium* in all monocultures and competition cultures. Average maximum density in monoculture was higher at 20°C than at 30°C irrespective of food level for *D. excisum*, but it was higher at 20°C than at 30°C for *D. dubium* only at low food level (Fig. 2a). Maximum growth rate was not directly affected by competition (ANOVA, $F_{1,32}=2.129$, $p=0.154$).

In both monoculture and competition experiments, *D. excisum* had higher r than *D. dubium* in all food and temperature combinations (Fig. 2b). At both higher temperature and food level, two species had higher r , whereas at both lower temperature and food level, two species had higher r (Fig. 2b). In the competition experiments, *D. excisum* always outcompeted *D. dubium* irrespective of food concentration at both 20°C and 30°C .

Discussion

The species distribution modeling confirmed that *D. dubium* dominates in subtropical and temperate regions, and *D. excisum* in tropical regions, and indeed they have a very narrow climate niche overlap. *D. excisum* always has higher intrinsic rate of population increase (fitness) and outcompeted *D. dubium* irrespective of food concentration within overlapping temperature niche.

Temperature niches and species distribution

The species distribution modeling shows the fundamental niches for both *D. dubium* and *D. excisum* are larger than their realized niches represented by few occurrence records. The temperature niche for tropical *D. excisum* was narrower than that of subtropical *D. dubium*. Failure of occurrence of the two species in America, North Europe, and North Africa may be due to their colonization history, dispersal restrictions, or their competition with temperate zooplankters, e.g. *Daphnia* [41–43].

Generally, temperature is an essential determinant in species' distribution [2, 10–13, 44–47]. Difference in the critical thermal minimum and maximum appears to be the basis for niche separation between *D. dubium* and *D. excisum* [25]. Due to its critical thermal minimum, the extension of *D. excisum* into subtropics is strongly limited. When the temperature falls below their critical thermal minimum, *Diaphanosoma* normally produces resting eggs to protect them from extinction and expand their distribution [22, 48]. Theoretically, *D. excisum* can produce resting eggs to preserve its population below 15°C, i.e. a temporal storage effect. If so, *D. excisum* can colonize new habitats even more northward, which is contradicted with its present distribution. Three reasons may account for *D. excisum*'s inability to expand its northward distribution, one of which is resting eggs viability, because hatching of resting eggs requires stimuli from specific temperature and photoperiod conditions [49]. Another is that the hatchlings from the potential resting eggs are simply outcompeted by populations of other *Diaphanosoma* species capable of overwintering in active stage, never allowing *D. excisum* populations to become established outside of tropics. A third one is that there may be other mechanisms (e.g. hybridization) rather than producing resting eggs for *D. excisum* to adapt to low temperature. During northward expansion, when encountering with *D. dubium*, *D. excisum* produces male clones to hybridize with female *D. dubium*. This can explain the observed hybrids of *D. excisum* and *D. dubium* in their distribution edge [49], which may have a higher fitness than their parental species [50–52].

Interspecific competition and species distribution

For *D. dubium*, its extension to tropics is limited. From our life history experiment (also see [25]) we know that both species can adapt to high temperature and so high temperature does not likely limit the southern extension of *D. dubium*. *D. excisum* outcompeted *D. dubium* in the exploitative competition irrespective of temperature and food in the competition experiments. Exploitation competition or interference competition during expansion is sufficient to account for parapatric distribution of two congeneric species [53, 54].

The maximum population density in monocultures is much higher for *D. excisum* than for *D. dubium*. Such result is expected only when *D. excisum* utilizes food more efficiently and has higher fitness. The

competitive superiority of *D. excisum* in our experiments is explained by its higher r , which allows it to monopolize available resources and thus gain a numerical advantage in the competition. High r is considered characteristic of tropical cladocerans [55]. *D. excisum* is a tropical species, and does possess higher r than *D. dubium* in the present study as well as previous experiment with a greater variety of clones of both species. The fast initial increase in abundance of *D. excisum* is especially critical in face of the lower maximum population density of *D. dubium*, producing strong suppression on *D. dubium* population growth.

D. excisum fully outcompeted *D. dubium* at all food concentrations when temperature ≥ 20 °C. It is thus reasonable to assume that this competition limits *D. dubium*'s spread into the tropics along with fish predation. In addition, high intensity of fish predation pressure in the tropics may aggravate the inferior competitive position of the larger sized *D. dubium* because visual-hunting predators or filter feeders actively or passively select for larger prey [56]. Achenbach and Lampert [57] also pointed out that the size shift from larger bodied to small bodied zooplankton in lakes occurred with increasing temperature due to the increase selective predation. The similar shift in body size was observed in an introduced goby species preying on large-sized zooplankton and aquatic insects [58]. Although the difference in body size for our congeneric species is rather small, the failure of the larger sized *D. dubium* when competing with the slight smaller *D. excisum* in the field may be attributed in part to such selective predation which persist all the year-round in tropical water.

Conclusions

In conclusion, as predicted by Janzen's hypothesis and the modern coexistence theory [10, 14], difference in thermal adaptation causes a narrow overlap of climate niches between two *Diaphanosoma* species. *D. excisum* has a narrower temperature niche and higher intrinsic rate of population increase in warm water. At ≤ 15 °C, *D. excisum* can not maintain its active population, and is therefore limited to tropics. The temperature is not the physiological factor limiting *D. dubium*'s extension into tropics; however at ≥ 20 °C, *D. excisum* outcompetes *D. dubium* and limits its spread to the south. Stable temperature niche difference overcoming fitness inequality in food dimension explains the parapatric distribution pattern for the two competitive congeneric species.

Declarations

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Authors' contributions

BPH and FP designed the study. ZW, PY, and QH performed the experiment. JL and PL analyzed the data with substantial advice and direction from BPH and HD. PL, BPH and HD wrote and corrected the manuscript. PL, PY and ZW conducted all field work and collected all samples with assistance from FP. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article and its additional files.

Ethics approval and consent to participate

Sampling and all work did not have any visible adverse effects on zooplankton in natural waters. No any permissions or ethics approval are required for sampling and monitoring zooplankton in lakes and reservoirs. Our field sampling follows and obeys Wildlife Protection Law of the People's Republic of China (revised in 2018).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Tables

Table 1 The Boyce Index for four predicted models (bioclim, brt, glm, rf) to depict the ordered rank of predicted expected ratio along suitability.

Species	Boyce Index for selected models			
	bioclim	brt	glm	rf
<i>D. dubium</i>	-0.081	0.486	0.926	0.883
<i>D. excisum</i>	0.415	0.497	0.906	0.805

Table 2 ANOVA tests of the effect of species (*D. dubium* or *D. excisum*), temperature (20 or 30°C), food concentration (0.5 or 1.0 mgC/L), competition and their interactions on the maximum population density, maximum growth rate (r_{max}) in 300 mL cultures. Shown are: F, p. Only significant values (p<0.05) were displayed.

SOURCE	Maximum population density		r_{max}	
	F _{1,32}	p	F _{1,16}	p
Species	302.475	0.000	15.551	0.001
Food	41.916	0.000	14.456	0.002
Temperature	5.203	0.029	96.938	0.000
Competition	28.069	0.000		
Species * Food	23.455	0.000		
Species * Temperature	31.140	0.000	6.744	0.019
Food * Temperature			33.572	0.000
Species * Food * Temperature	22.008	0.000		

Figures

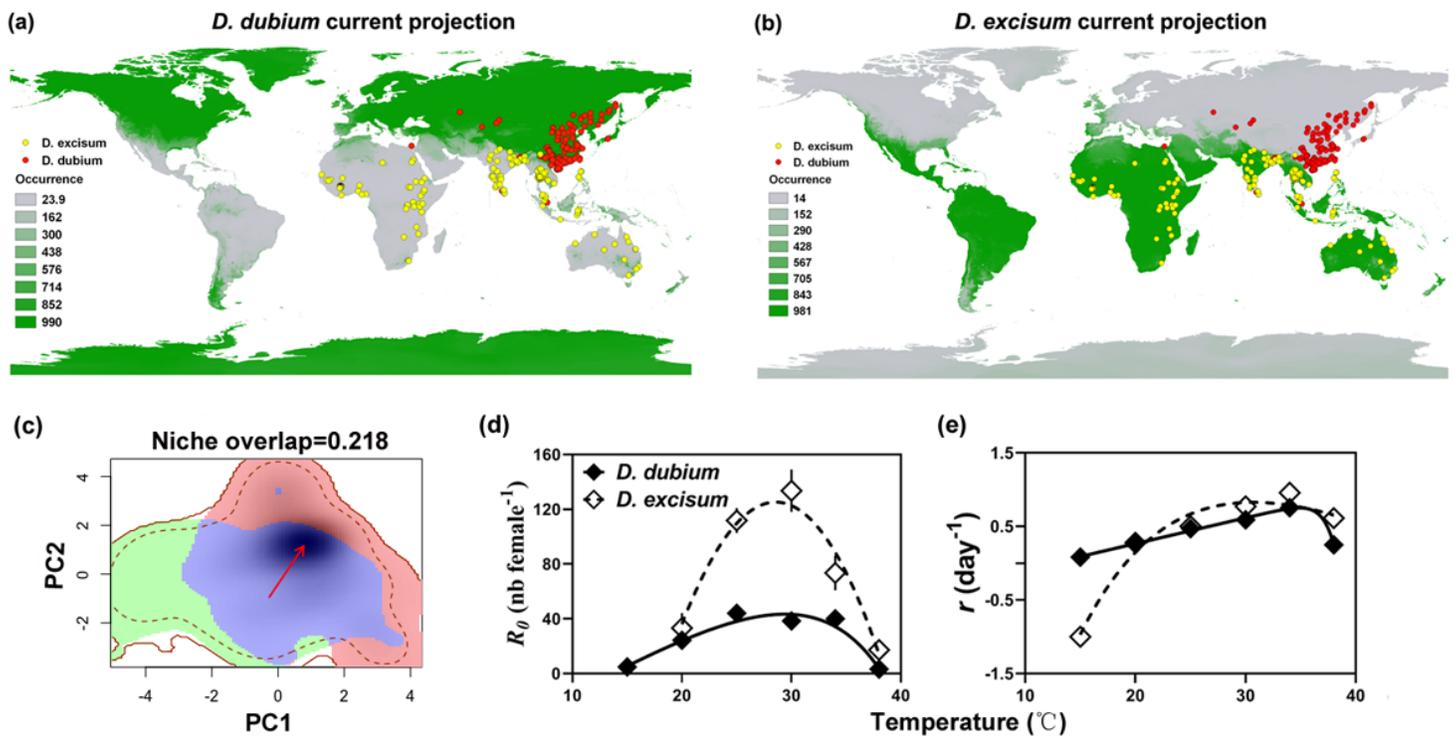


Figure 1

The potential distribution of *D. dubium* (a) and *D. excisum* (b) in current climate condition, and their temperature niches represented by net reproductive rate (R_0) (d) and the intrinsic rate of population increase (r) (e) for single clones. Their climate niche overlap under species distribution models was also displayed (c). The two maps (Fig.1a and 1b) were generated with 'ecospat' package in R 3.5.3, and visualized in QGIS v2.1. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

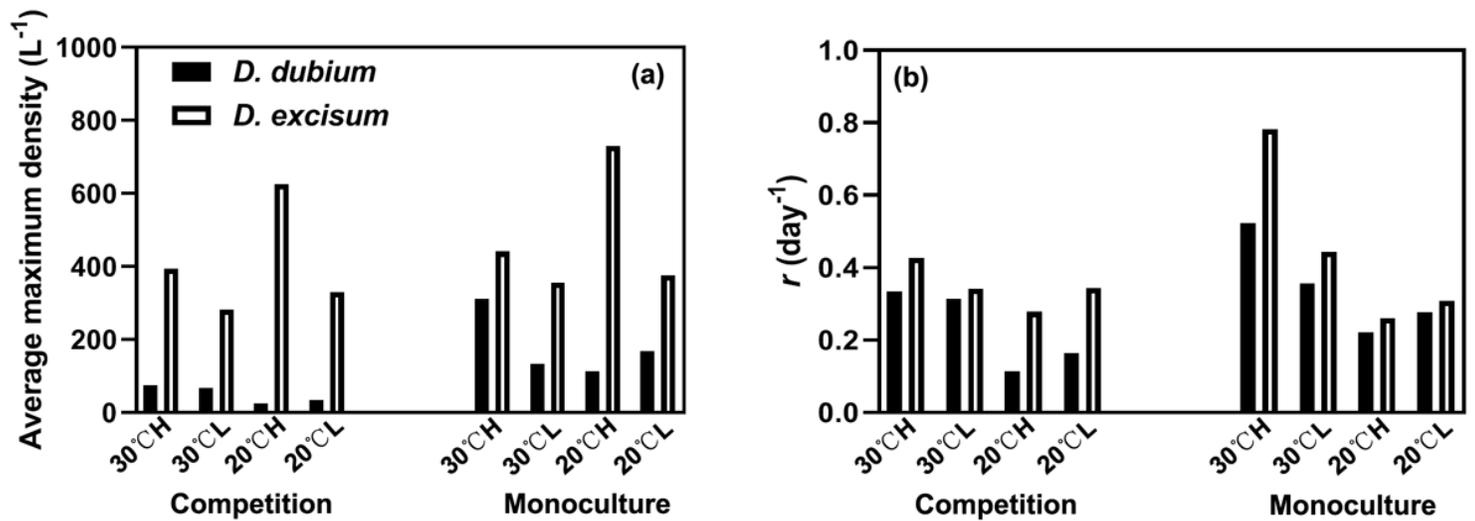


Figure 2

Average maximum population density (a) and r (b) at 30°C and 20°C under monocultures and competition cultures respectively. Letter H: high food level (1.0 mgC/L), letter L: low food level (0.5 mgC/L).

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