

Climate warming and selective adaptation to thermal refugia

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June 27, 2023

Abstract

The impact of climate warming on biodiversity loss is exacerbated not only by changes in mean but also by spatio-temporal variability in temperature. Access to refugia can mitigate the impact of thermal fluctuations amongst species. The effectiveness of refugia during periods of adverse warming scenarios, i.e., seasonal fluctuations, hotter-than-average summers, and warmer-than-average winters remains largely unexplored. Here, we study a bio-energetic consumer-resource model and identify the mixed success of refugia in maintaining species persistence and stability, depending on the amplitude of fluctuations, diverse warming scenarios, and species body size. Whilst refugia withhold otherwise inevitable extinction at high amplitude fluctuations in all the warming scenarios, at lower amplitudes, they may not provide similar benefits. This arises due to non-monotone thermal responses of their foraging efforts and monotonically increasing metabolic requirements. The qualitative difference among thermal responses leads to more energy losses rather than gains at low amplitudes. We find that refugia are most beneficial during hotter summers and least during typical seasonal fluctuations. Our results also suggest that refugia can be more favourable to species in temperate and Mediterranean regions, unlike those inhabiting tropical regions. We also consider an extreme heat wave event and observe that small-bodied species can counteract their negative effects by seeking refuge at low amplitudes. Overall, our work hints at selective adaptation to refugia - conditioned on the aggregated effect of thermal conditions of the local habitat and species body size - as a mechanism for biodiversity maintenance.

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[†]This article contains supplementary materials.

Abstract

The impact of climate warming on biodiversity loss is exacerbated not only by changes in mean but also by spatio-temporal variability in temperature. Access to refugia can mitigate the impact of thermal fluctuations amongst species. The effectiveness of refugia during periods of adverse warming scenarios, i.e., seasonal fluctuations, hotter-than-average summers, and warmer-than-average winters remains largely unexplored. Here, we study a bio-energetic consumer-resource model and identify the mixed success of refugia in maintaining species persistence and stability, depending on the amplitude of fluctuations, diverse warming scenarios, and species body size. Whilst refugia withhold otherwise inevitable extinction at high amplitude fluctuations in all the warming scenarios, at lower amplitudes, they may not provide similar benefits. This arises due to non-monotone thermal responses of their foraging efforts and monotonically increasing metabolic requirements. The qualitative difference among thermal responses leads to more energy losses rather than gains at low amplitudes. We find that refugia are most beneficial during hotter summers and least during typical seasonal fluctuations. Our results also suggest that refugia can be more favourable to species in temperate and Mediterranean regions, unlike those inhabiting tropical regions. We also consider an extreme heat wave event and observe that small-bodied species can counteract their negative effects by seeking refuge at low amplitudes. Overall, our work hints at selective adaptation to refugia - conditioned on the aggregated effect of thermal conditions of the local habitat and species body size - as a mechanism for biodiversity maintenance.

Keywords: thermal fluctuations, refugia, warming scenarios, extreme events, species persistence

23 Introduction

24 Climate change is one of the pivotal subjects of our time. Reportedly, phenology, distribution,
25 and many other determinants of species interactions are constrained by global climate change
26 ([Parmesan and Yohe 2003](#), [Deutsch et al 2008](#)). Amongst numerous components of climate,
27 the increasing temperature is one of the major abiotic factors leading to global warming,
28 and threatening resource conservation and management ([Hughes 2000](#), [Walther et al 2002](#),
29 [Vasseur and McCann 2005](#), [Tylianakis et al 2008](#), [Rall et al 2010](#), [Binzer et al 2012](#), [Kaur](#)
30 [and Dutta 2020, 2022](#)). Importantly, climate warming along with changes in the long-term
31 mean temperature is accompanied by irregular patterns of thermal fluctuations, across space
32 and time ([Chen et al 1999](#), [Vasseur et al 2014](#), [Lawson et al 2015](#)). Spatial variability in
33 temperature is an important driver that can lead to shifts in species' ecological niches ([Sinervo](#)
34 [et al 2010](#), [Chappon and Seuront 2011](#)). However, there exists a paucity of comprehensive
35 understanding regarding the role of thermal variability across diverse regions in facilitating
36 species persistence and enabling effective climate change adaptation. In general, adaptation
37 to climate warming has been prevalent in several species in nature through movement for
38 a period ranging from a day to months, to a habitable location termed as thermal refugia
39 ([Ashcroft 2010](#), [Keppel et al 2012](#)).

40 Refugia have been distinguished as regions or habitats that can support populations, par-
41 ticularly, to which species can withdraw, persevere in, and in this way sustain, under changing
42 environmental circumstances ([Ashcroft 2010](#), [Keppel et al 2012](#), [Keppel and Wardell-Johnson](#)
43 [2012](#)). The movement to thermal refugia has been studied for species whose body tempera-
44 ture is often directly linked to vital rates at the organismal and population levels. Thermal
45 refugia can provide a feasible habitat to thermo-regulatory species in either way: species
46 may relocate themselves to a cool territory to reduce their body temperatures ([Scheffers](#)
47 [et al 2014](#)) or to warm regions (basking arena) to increase thermo-regulation during outa-
48 geous climatic circumstances ([Sears and Angilletta Jr 2015](#)). Therefore, refugia can expand
49 the exhibition of a life form by permitting admittance to areas that enhance individual

environmental and physiological capacities (Li et al 1995, Stewart and Lister 2001). For example, endangered Egyptian tortoise (*Testudo kleinmanni*) abode larger shrubs during the activation season to ameliorate fluctuating environments (Attum et al 2013). While many temperate species encountered extinctions and Southwards range shifts during the Quaternary glacial periods, geographic distributions indicated the persistence of western European species in refugia (Culling et al 2006). Sinervo et al (2010) demonstrates that in an endeavour to stay away from infeasible thermal variability, Sceloporus reptiles retreat to cool refugia. Despite beneficial allocation to refugia reported in the aforementioned studies, it is imperative to understand how movements to refugia under spatial thermal variability regulate species abundance subject to different warming conditions.

To comprehend how changes in temperature fluctuations affect populations in various habitats, it is important to examine how these changes impact the growth and survival of species. These temperature variations can either work together with or independently from the mean temperature, making it crucial to investigate their interplay and potential consequences. For instance, the effect of changing mean temperature on the physiological performance of terrestrial species is aggravated by irregular thermal fluctuations (Deutsch et al 2008, Paaijmans et al 2013, Clusella-Trullas et al 2011). Cabrerizo and Marañón (2021) have shown that thermal variations might suppress the effect of changing mean temperature on cellular organisms' ability to store nutrients. While in some instances, fluctuations in population abundance may be amplified irrespective of changes in the mean temperature, leading to increased risks of species extirpation.(Bjørnstad and Grenfell 2001, Boyce et al 2006, Ovaskainen and Meerson 2010). Therefore, knowledge of the mean-variance interplay of temperature is vital for understanding species' biological processes with access to thermal refugia.

Further, it is important to map various climatic scenarios associated with changing warming conditions upon ecological interactions. A recent report (Change 2018) highlights that climate warming leads to warmer-than-average winters and hotter-than-average summers.

Evidently, there are still a few gaps in the understanding of the climate warming scenarios and adaptability to refugia. First, past studies investigating functional stability and biodiversity of consumer-resource systems did not incorporate thermal variability accounting for these projected climate change scenarios. Second, understanding the impact of different climate scenarios on species persistence is equally important. It is majorly unknown how variation in warming conditions determines the usefulness of retreating habitats/refugia in promoting species persistence. Third, recent studies have discussed the consequences of marine heat waves on refugia (Mo et al 2022, Verdura et al 2021), while others have anticipated the loss of refugia in marine ecosystems with increasing global warming by the end of the century (Dixon et al 2022, Oliver et al 2019). However, studies concerning the impacts of high thermal stress on consumer-resource interaction and their refugia are lacking. Particularly, the utility of thermal refugia also needs to be investigated in periods of extreme thermal stress, i.e., heat wave events (Kunze et al 2022). Identifying thermal refugia amidst periods of climate-induced stress can have pragmatic biodiversity management implications.

In this study, we consider a bio-energetic model of consumer-resource interactions inhabiting thermally varying conditions, viz., typical seasonal fluctuations, hotter summers, and warmer winters. We incorporate a mechanistic explanation of how species' biological traits shape their response towards warming and the consequent impact of refugia in each of the warming conditions. We find that the type of warming scenarios, the amplitude of temperature fluctuations (classified as low, intermediate, and high), and the species body size are crucial factors in determining the effectiveness of refugia as retreat habitats that mitigate the impact of warming. While relocating to thermal refugia can maintain biodiversity at high amplitudes of fluctuations and low mean temperatures, its potency at intermediate and lower amplitude decreases, subject to the warming scenarios. At intermediate amplitudes of temperature fluctuations, relocating to refugia is more beneficial to enhance the persistence of species experiencing hotter summers, than warmer winters and typical fluctuations. Consequently, the effectiveness of refugia also varies based on the latitude of the species'

habitat, with temperate and Mediterranean regions characterized by greater temperature fluctuations and lower mean temperatures, exhibiting a higher utility of refugia compared to tropical regions.

Materials and Methods

Projected climate warming scenarios

Global warming leads to an elevation in the mean annual temperature and alterations in the seasonal thermal fluctuations (Change 2018). In this work, we consider three distinct thermal scenarios: (I) Typical seasonal fluctuations; where the daily mean and amplitude of temperature remain unchanged, (II) Warmer winters; this scenario represents that the daily increase in the minimum temperature is faster than the daily increase in maximum temperature, hence mean increases over time but amplitude decreases, and (III) Hotter summers; when both mean and amplitude increase over time because an increase in the maximum temperature is faster than an increase in the minimum temperature.

A temperature-dependent consumer-resource model

We study the dynamics of a bio-energetic consumer-resource (C - R) model (Yodzis and Innes 1992) that incorporates temperature-dependent phenotypical responses when exposed to the above-mentioned warming scenarios. The model is given below:

$$\frac{dR}{dt} = r(T_R)R(1 - q(T_R)R) - a_C(T_C)\frac{RC}{R + R_h}, \quad (1a)$$

$$\frac{dC}{dt} = \left(e_C a_C(T_C) \frac{R}{R + R_h} - m_C(T_C) \right) C, \quad (1b)$$

where the basal resource (R) exhibits logistic growth with per-capita intrinsic growth rate r and intraspecific competition $q = \frac{1}{K}$, as a function of the resource body temperature T_R , where K is the carrying capacity. The consumer's phenotypical parameters, i.e., the attack rate a_C , and metabolic rate m_C depend upon its body temperature T_C (see Supplementary Information SI-1.1, Fig. SI-1.1). C follows the Holling Type-II functional response (Murdoch

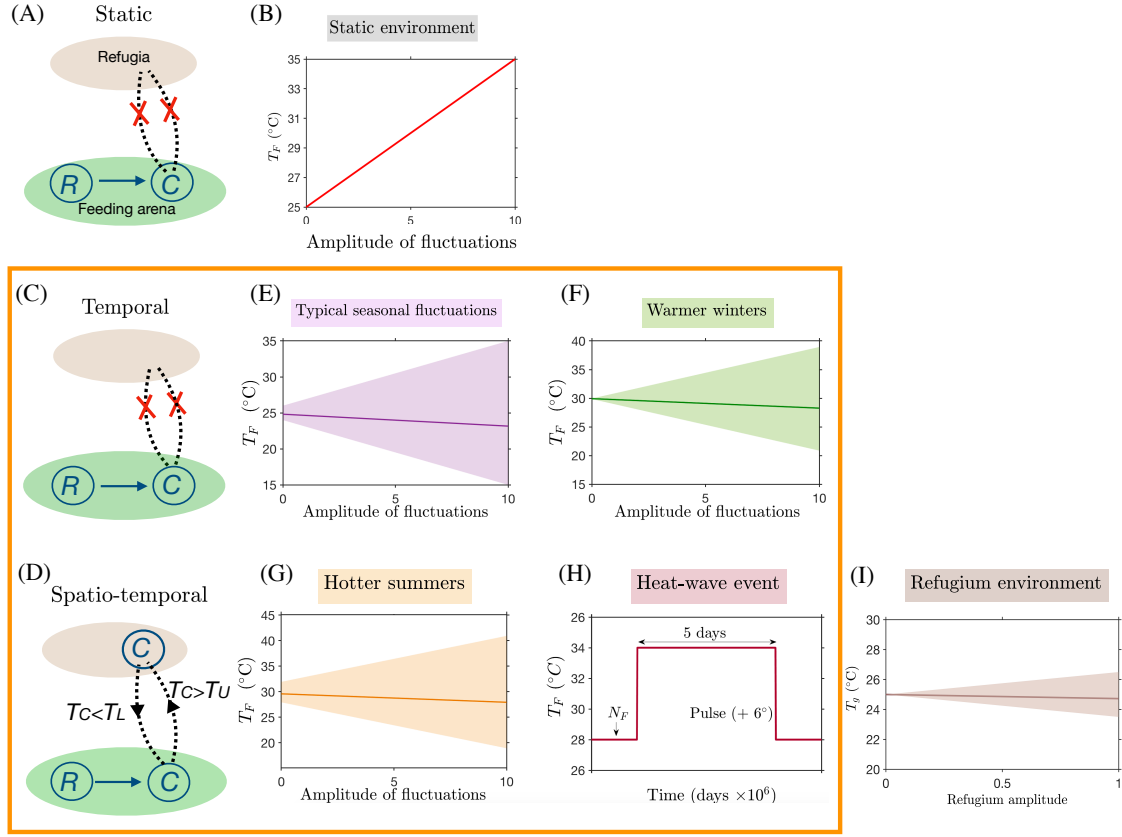


Figure 1. Consumer–resource interactions in habitats with the thermally variable environment. (A)–(B) A static habitat where the temperature in the feeding region (T_F) remains constant, (C) temporal habitat, and (D) spatio-temporal habitat. Temperature profiles in the habitats experiencing (E) typical seasonal fluctuations, (F) warmer-than-average winters, (G) hotter-than-average summers, and (H) a heat wave event of 5 days generated when $\sigma_F = 5^\circ\text{C}$ (amplitude of fluctuation). (I) The refugium allows heterogeneity in the thermal fluctuations (T_g) experienced by the consumer and the resource. The solid line in the sub-figures ((E), (F), (G), and (I)) represents the mean temperature, while the shaded region depicts the maxima and minima of the thermal fluctuations. The orange box encloses all the combinations of habitat type and warming condition we have studied in this work. In (A), (C) and (D), arrows between R and C determine the direction of energy flow from the resource to the consumer. Parameter values: $\alpha = 4$ and $\beta = 6$ for warmer winters, and $\alpha = 6$ and $\beta = 4$ for hotter summers. All the other parameter values are obtained from Table 1 (see supplementary).

et al 2003) having half-saturation constant R_h . Following (Vasseur and McCann 2005, Amarasekare and Coutinho 2014, Uszko et al 2017, Custer 2005), in our model the conversion efficiency e_C and the half-saturation constant R_h remain unaltered by temperature.

Here, the consumer and the resource, at first, reside in the feeding area with a time-

130 dependent temperature profile $T_F(t)$ such that:

$$T_F(t) = (N_F + mt) + (\sigma_F + at) \sin\left(\frac{t}{p}\right), \quad (2)$$

131 where N_F denotes the mean habitat temperature of the feeding area having an amplitude
 132 of the fluctuations as σ_F . p scales the recurrence of the thermal fluctuations. The different
 133 warming scenarios are incorporated in the feeding area by modulating the values of daily
 134 variation in mean m and amplitude a . Here, $m = \frac{\text{Max}_T + \text{Min}_T}{2}$, and $a = \frac{\text{Max}_T - \text{Min}_T}{2}$.
 135 The quantities $\text{Max}_T = \frac{\alpha}{365 \times n}$ and $\text{Min}_T = \frac{\beta}{365 \times n}$, respectively, show the degrees by which
 136 the maximum and the minimum temperatures have risen over n years (1 year=365 days)
 137 ([Amarasekare 2019](#)).

138 Depending upon the temperature profile T_F (Eqn. (2)) and the accessibility to a refugium
 139 arena, the feeding arena is classified as static, temporal, and spatio-temporal. Static condi-
 140 tions reveal no temporal variation in T_F (i.e., $m = 0$ and $a = 0$) and the consumer does not
 141 move to the refugium (see Figs. 1(A)-1(B)). Temporal and spatio-temporal conditions are
 142 characterised by thermal variability across time (non-zero m and a) (see Figs. 1(E)-1(G)).
 143 However, the spatio-temporal habitat in addition allows the consumer to relocate into a
 144 refugium arena (see Fig. 1(D)) having temperature profile T_g as below:

$$T_g(t) = N_F + \sigma_F A_g \sin\left(\frac{t}{p}\right) + N_g, \quad (3)$$

145 where, N_g moves the temperature of the refugium above or beneath the temperature of the
 146 feeding arena. $0 \leq A_g \leq 1$ is a scaling factor demonstrating the sufficiency of the refugium
 147 via amplitude of temperature oscillations in the feeding region ([Fey and Vasseur 2016](#)).

148 Frequently, refugia exist in territories with poor or no food assets, like underground
 149 passages. For example, lizards access refugia from hot and dry environments by covering
 150 themselves underground to the detriment of not consuming prey ([Rohr and Palmer 2013](#)).
 151 Likewise, cold-intolerant Florida manatee (*Trichechus manatus latirostris*) forsake scavenging

152 during cold water temperatures (Haase et al 2020), and Bevelhimer and Adams (1993)
 153 demonstrated that kokanee salmon accomplish cooler temperature levels to the detriment of
 154 being spatially isolated from their resources. Therefore, the resource remains stationary and
 155 equilibrates quickly with the surrounding temperature, that is:

$$T_R = T_F, \quad (4)$$

156 but the consumer compromises between resource acquisition and performance optimisation
 157 while accessing the refugia. Particularly, as long as the consumer maintains its body tem-
 158 perature (T_C) below an upper threshold T_U , it forages in the feeding area. Beyond T_U , the
 159 consumer retreats to the refugium until the temperature drops to the lower limit, T_L , followed
 160 by which it returns to the feeding area and resumes foraging there (Stevenson 1985, Cowles
 161 and Bogert 2006). Therefore, the consumer body temperature depends upon its location
 162 (L_t) and the temperature profile of that location, determined by Newton’s law of cooling as:

$$\frac{dT_C}{dt} = \frac{1}{Q} (L_t T_F + (1 - L_t) T_g - T_C), \quad (5)$$

163 where L_t is a step function taking value 1 when the consumer is in the feeding area, and 0 if it
 164 retreats to the refugium. Therefore, L_t is always 1 in the case of static and temporal habitats.
 165 Nonetheless, in the case of the spatio-temporal condition, the consumer may regulate its
 166 body temperature by switching L_t from 1 to 0 (or vice-versa) and experience temperature
 167 fluctuations in the refugium arena with the same frequency but varying amplitude than the
 168 feeding area. Q is the thermal time constant which depends upon the consumer body size
 169 (M_C) as $Q = \exp^{0.72} M_C^{0.36}$ (Grigg et al 1979).

170 The minimum and maximum temperatures in the static habitat coincide with the mean
 171 temperatures and vary from 25 °C to 35 °C along variations in σ_F (Fig. 1(B)). The mean
 172 temperatures in typical seasonal fluctuations are low (changes from 25 °C to 23 °C, along
 173 with increasing σ_F (Fig. 1(E)). Nonetheless, warmer winters and hotter summers, respec-

tively lead to higher mean temperatures ranging from 30 °C to 28 °C (Figs. 1(F)-1(G)). The refugium, on the other hand, retreats the consumer to a cooler temperature regime with a mean of ≈ 25 °C and no fluctuations to diel fluctuations between 24 °C to 26 °C (Fig. 1(I)).

Extreme heat wave condition

We also explore the utility of thermal refugia on species persistence during periods of extreme heat wave events. A heat wave condition is characterized by the mean value of the habitat temperature crossing a threshold temperature for 3 or more number of days consecutively (Kovats and Hajat 2008, Kunze et al 2022). Figure 1(H) demonstrates that during a heat wave event, the feeding region exhibits no temporal thermal variability (as in the static case). Rather, experiences a temperature pulse at a difference of 6 °C, for 5 consecutive days (Kunze et al 2022), and for each amplitude of fluctuation. To examine the importance of the refugium arena during heat stress periods on consumer-resource dynamics, we consider cases: (i) without refugium; where the consumer cannot relocate to a cooler habitat, and (ii) with refugium. More explicitly, we investigate the impact of a heat wave on small-body-sized and large-body-sized organisms.

We simulate population time series for 100 years and record population dynamics in the final 3 years for each amplitude of fluctuation (σ_F) varying in the range 0 – 10 °C. For the sake of simplicity, we define the amplitude of fluctuations $\sigma_F \approx 4$ °C and below as low, σ_F in the range $\approx 4 - 7$ °C as intermediate, and $\sigma_F \approx 7$ °C and above as high. To set a frame of reference, we first study the population dynamics under static habitat (no temporal variability and no access to refugia). We then comprehend how variations in species' thermal regimes and access to the refugium arena during infeasible warming conditions impact the stability and persistence of the considered ecosystem. We use an aggregate approach which is based on evaluating individual-level parameters governing energy flux within an interaction to determine population-level measures (Yodzis and Innes 1992) (see Supplementary Information SI-1.2, Eqns. S.3-S.4). In addition, we perform stability analyses to comprehend how identifying thermal refugia can impact system's ability to recover from

tiny perturbations. Followed by which we measure the robustness of our outcome for different system parameters through sensitivity analyses.

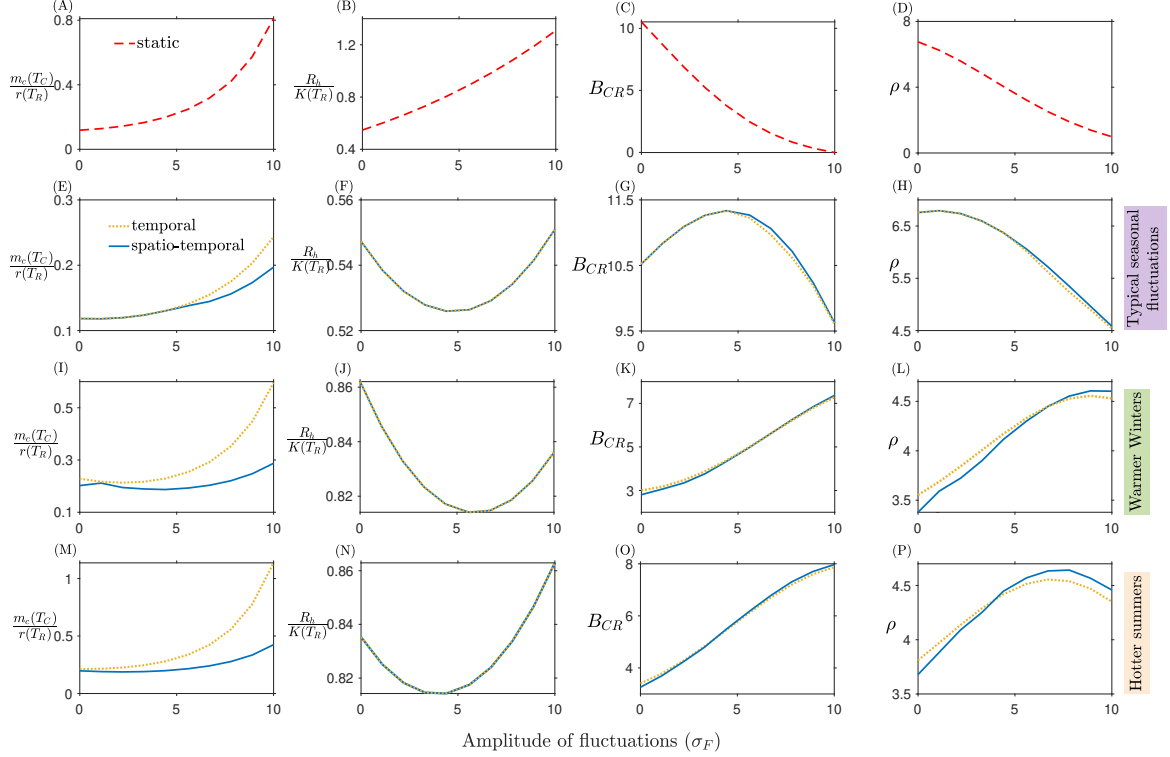


Figure 2. Thermal response of species physiological traits governing energy flux within the interaction as a function of the amplitude of fluctuation (σ_F). Each panel from left to right corresponds to the $\frac{m_C(T_C)}{r(T_R)}$, $\frac{R_h}{K(T_R)}$, Interaction strength (B_{CR}), and the gain-to-loss ratio (ρ) for (A)-(D) static habitats. Also for temporal and spatio-temporal habitats experiencing (E)-(H) typical seasonal fluctuations, (I)-(L) warmer-than-average winters, and (M)-(P) hotter-than-average summers. The parameter values are the same as in Fig. 1.

Results

Considering the thermal response functions of species across combinations of the 3 different thermal habitats and the 3 different warming scenarios (see Fig. 2), we study how the amplitude of fluctuations (σ_F) affect species persistence, and the role of refugia, if any, in enhancing it. We observe that the consumer abundance in the static habitat declines along the increase in the amplitude irrespective of the warming scenarios (Figs. 3(A), 3(D), and 3(G)). This arises due to the monotonic response of its metabolic needs (Fig. 2(A)), depleting interaction strength (B_{CR}) between the species, and decline in attacking efficiencies of the consumer to

gain energy from the resource (Figs. 2(B) and 2(D)). Meanwhile, the resource abundance is elevated at high temperature fluctuations on account of reduced resource accumulation by the consumers (Figs. 3(B), 3(E), and 3(H)). In the next sections, we find the conditions under which retreating to refugia is practical for species across thermally varying warming scenarios and provide a rationale for the same.

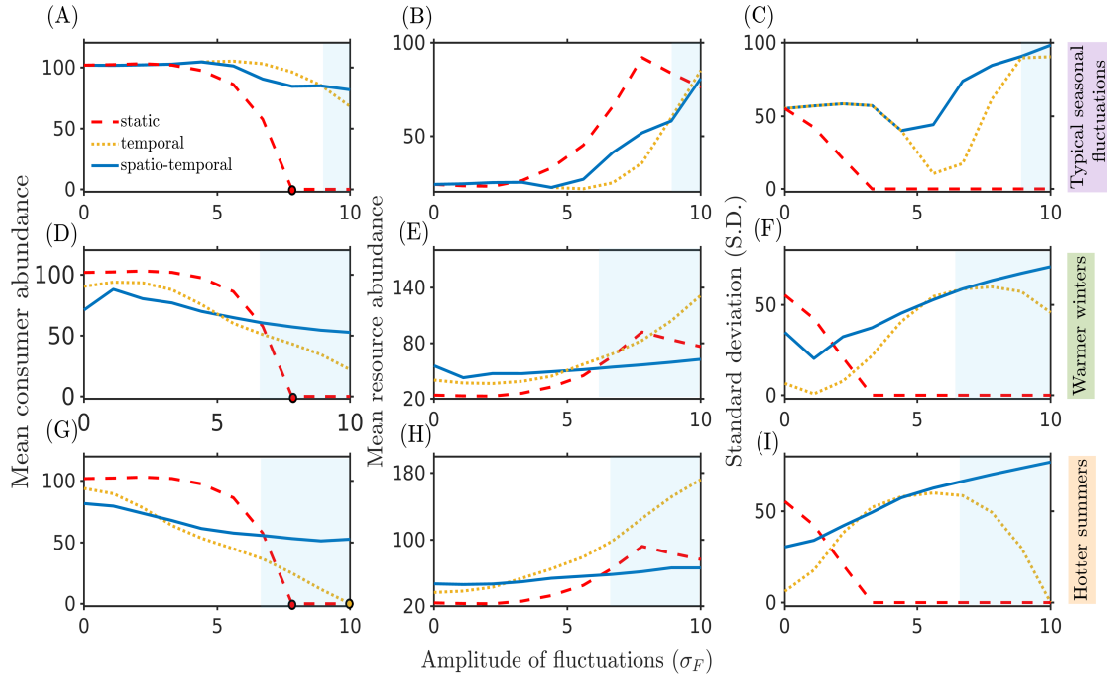


Figure 3. Impact of thermal variability on the consumer-resource dynamics experiencing different warming scenarios and habitat conditions. For each climate warming scenario (A), (D) and (G) depict the mean of the consumer abundance, (B), (E) and (H) represent the mean of the resource abundance, and (C), (F) and (I) is the standard deviation (S.D.) of fluctuations in consumer abundance. Dashed red lines correspond to the static habitat, and dotted yellow lines and solid blue lines correspond to the temporal and spatio-temporal habitats, respectively. The shaded region depicts the range of σ_F for which moving to the refugia is most beneficial in maintaining consumer abundance.

Significance of refugia when the feeding region experiences typical seasonal fluctuations

At low σ_F , the aggregate phenotypes within the consumer-resource interaction depict similar responses in each of the temporal and spatio-temporal habitats, as observed in the static case (Figs. 2(A)–2(H)). Therefore, thermal variability and access to refugia at low amplitudes of fluctuations do not significantly impact species persistence. In comparison to the static, both temporal and spatio-temporal conditions at $\approx 5^\circ\text{C}$ lead to higher attacking effi-

ciency (Fig. 2(F)) of the consumer accompanied by its stronger interaction with the resource. This provides energetic gains to the consumer and thus lowers the resource abundance at temperatures $\approx 24.8\text{ }^{\circ}\text{C}$ – $25\text{ }^{\circ}\text{C}$ (Fig. 3(B)).

However, further elevation in σ_F leads to a decrease in the interaction strength (Fig. 2(G)), yet the resource enrichment ratio increases (Fig. 2(F)). Thereupon, at high amplitudes resource abundance increases and consumer abundance declines. Notably, at intermediate values of σ_F , the temporal case maintains the highest consumer abundance followed by the spatio-temporal and static counterparts. The consumer is most abundant in the spatio-temporal case only at higher values of σ_F ($\approx 9\text{ }^{\circ}\text{C}$). In addition, the consumer relocating in the refugium arena experiences high fluctuations in its abundance as compared to the case without the refugium (Fig. 3(C)). Thus access to refugia does not significantly enhance species persistence, unless at very high thermal variability.

Significance of refugia during warmer winters in the feeding region

When the feeding region experiences warmer-than-average winters, the consumer experiences higher body temperatures than in the seasonal environment. Thus, in comparison to seasonal fluctuations, here, the consumer exhibits an increase in energetic losses to its metabolic requirements (Fig. 2(I)) and perceives lesser resource due to a declining resource enrichment ratio (Fig. 2(J)).

At low values of σ_F , therefore, a static environment is most profitable to sustain consumer abundance at low amplitudes (Fig. 3(D)). Increasing σ_F decreases the mean abundance of the consumer such that the temporally variable habitat are better (in terms of maintaining community ratio) than its spatio-temporal counterpart with access to the refugium, followed by the static habitat. Further, the difference in the ratio $\frac{m_C(T_C)}{r(T_R)}$ for temporal and spatio-temporal habitats increases significantly along σ_F , revealing higher metabolic requirements in the temporal case (Fig. 2(I)). Simultaneously, the consumer's energetic gain is high while it can move between the feeding region and the refugium (Fig. 2(L)). Consequently, for high thermal fluctuations at the feeding area, moving to the refugium can be beneficial to the

consumer population.

Significance of refugia during hotter summers in the feeding region

The mean temperatures during the hotter-than-average summers are similar to the mean habitat temperatures during warmer winters. Nonetheless, in this case, the increase in daily mean and daily amplitude of fluctuations together depicts the reduced abundance of the consumer (Fig. 3(G)). Unlike the aforementioned thermal scenarios, here, the static environment is better in maintaining species abundance than the other two habitat conditions even at intermediate values of σ_F (Fig. 3(G)). Because of elevated metabolic demands (Fig. 2(M)), lowered energetic gains (Fig. 2(P)), and attacking efficiency (Fig. 2(N)) in temporal and spatio-temporal case, the consumer abundance declines even in the presence of the refugium arena. The overall community ratio is also disrupted at higher temperature fluctuations. Thus, relocating to cooler habitats when the feeding arena exhibits low amplitude of fluctuations may impede species persistence.

On the other hand, on adapting to the thermal refugium in the intermediate range of thermal fluctuations, the consumer attains lower metabolic requirements and obtains increased net energetic gain. At $\sigma_F \approx 10$ °C (Fig. 3(G)), temporal thermal variability in the feeding region leads to the consumer extirpation and resource reaches its self-limitation (Fig. 3(H)). This however is buffered when the consumer switches between the feeding region and the refugium. The fluctuation in species abundance decreases (increases) along σ_F , in temporal (spatio-temporal) regions (Fig. 3(I)). Identifying retreating habitats during hotter summers is, therefore, crucial for species persistence.

Consumers' performance and resource acquisition trade-off

On retreating to the refugium, the consumer attains lower metabolic requirements, however, at the cost of resource unavailability. This performance-acquisition trade-off due to the movement of the consumer is a keystone for community persistence. The consumer spends nearly 20% of its time in the refugium arena during a typical seasonal environment, at high

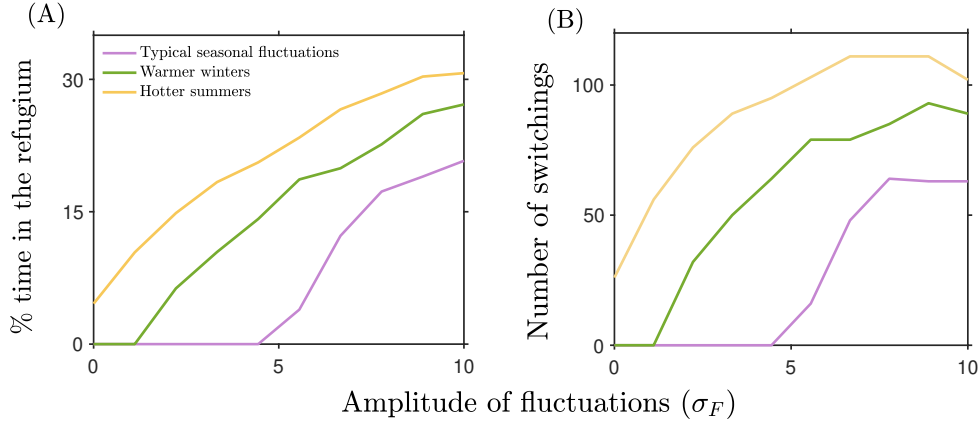


Figure 4. The impact of warming scenarios towards accessibility to the refugium. (A) The percentage of the time spent by the consumer in the thermally retreating habitat, and (B) the count of commutation/switching by the consumer between the feeding region and the refugium.

amplitudes of fluctuations. The amount of time spent by the consumer is $\approx 23\%$ in the case of warmer winters. Increased duration in the refugium arena leads to the reduced net flux of energy from the resource to the consumer, thus leading to decreased abundance. This explains the reason why warmer winters are more detrimental than the typical seasonal scenario. A similar argument follows for the hotter summers, as the time spent in this case is $\approx 30\%$ (see Fig. 4). An increase in the time spent by the consumer in the refugia detracts the consumer from energetic gains and can lead to its extinction. Therefore, the consumer must reside in the feeding region for sufficient time to buffer the thermal fluctuations in the feeding region along with optimisation of its performance and resource acquisition.

The impact of extreme heat wave event on the C-R interaction

We observe that the effectiveness of refugia during heat wave events at low amplitudes is contingent upon the body size of the species. The impact of stress caused by a heat wave event is more severe for the consumer with smaller body size, and access to refugia can propitiously act as an escape (Fig. 5(A)). However, the larger consumer do not experience notable advantages in relocating to thermal refugia during these events (Fig. 5(D)). The benefit obtained by small body-sized species is that small body-sized species have lower

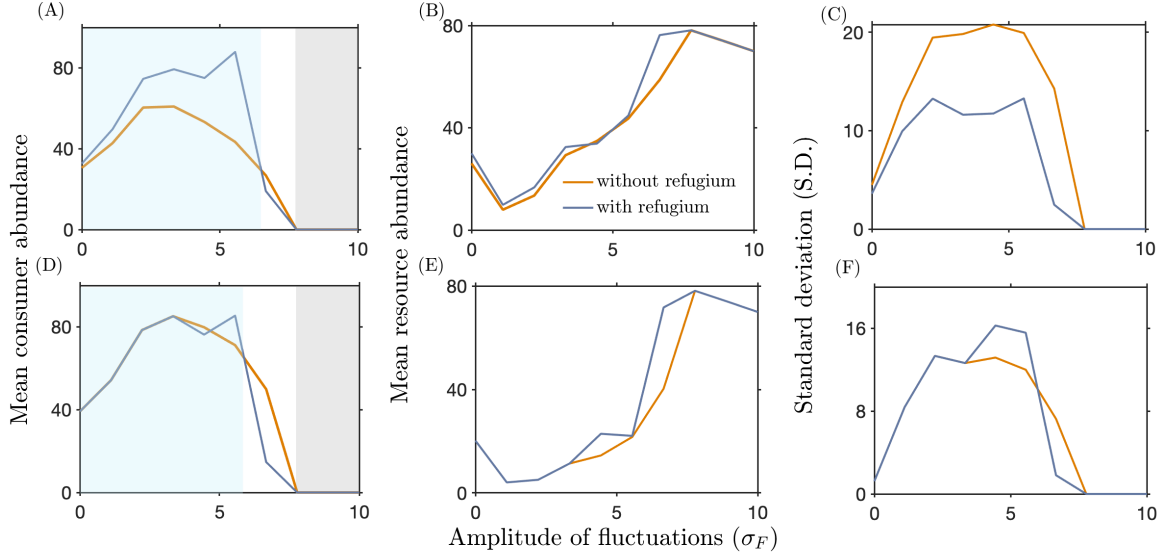


Figure 5. Impact of thermal variability on the consumer-resource dynamics experiencing a heat pulse for 5 consecutive days. Panels correspond to the species mean abundance, the community ratio and the standard deviation (S.D.) in their abundance for the (A)-(C) small body-sized ($M_C = 50$), and (D)-(F) large body-sized ($M_C = 500$) consumer. The blue shaded region corresponds to the amplitude range for which the refugium maintains higher consumer abundance. The grey shaded region corresponds to the amplitude range where the consumer undergoes extinction.

metabolic requirements. Therefore, it trades off between the metabolic demands and the resource accumulation such that the energetic losses are suppressed by the energetic gains. As the amplitude of thermal fluctuations increases (beyond ≈ 7 °C), the consumer irrespective of its body size gains no significant benefit of accessibility to the refugium. This is mainly because, at high amplitudes, due to the monotonic temperature response of metabolism and unimodal temperature response of the attack rate, the consumer exhibits lower attacking capabilities but higher energetic requirements. This further leads to the annihilation of the consumer population due to starvation at high temperatures, followed by which the resource abundance reaches its carrying capacity (Figs. 5(B) and 5(E)). We also note that the fluctuations in abundance of the small body-sized consumer are lower when they can move to the refugium as compared to the case without the refugium (Fig. 5(C)). Accessibility to the refugium, however, depicts the negligible difference in fluctuations in the abundance of the large-sized consumer (Fig. 5(F)). In all, movement to a thermal refugium during the

period of heat waves can benefit the persistence of small-sized species at low to intermediate amplitudes of thermal fluctuations. However, it may not buffer the detrimental impact of warming at the higher amplitude of fluctuations for small-bodied as well as large-bodied species.

Sensitivity analysis

In this section, we analyse our outcome for varying sets of ecological parameters. We find that our outcome is robust to changes in the individual-level phenotypical parameters (see Supplementary Information SI-1.3, Figs. SI-1.2-SI-1.9).

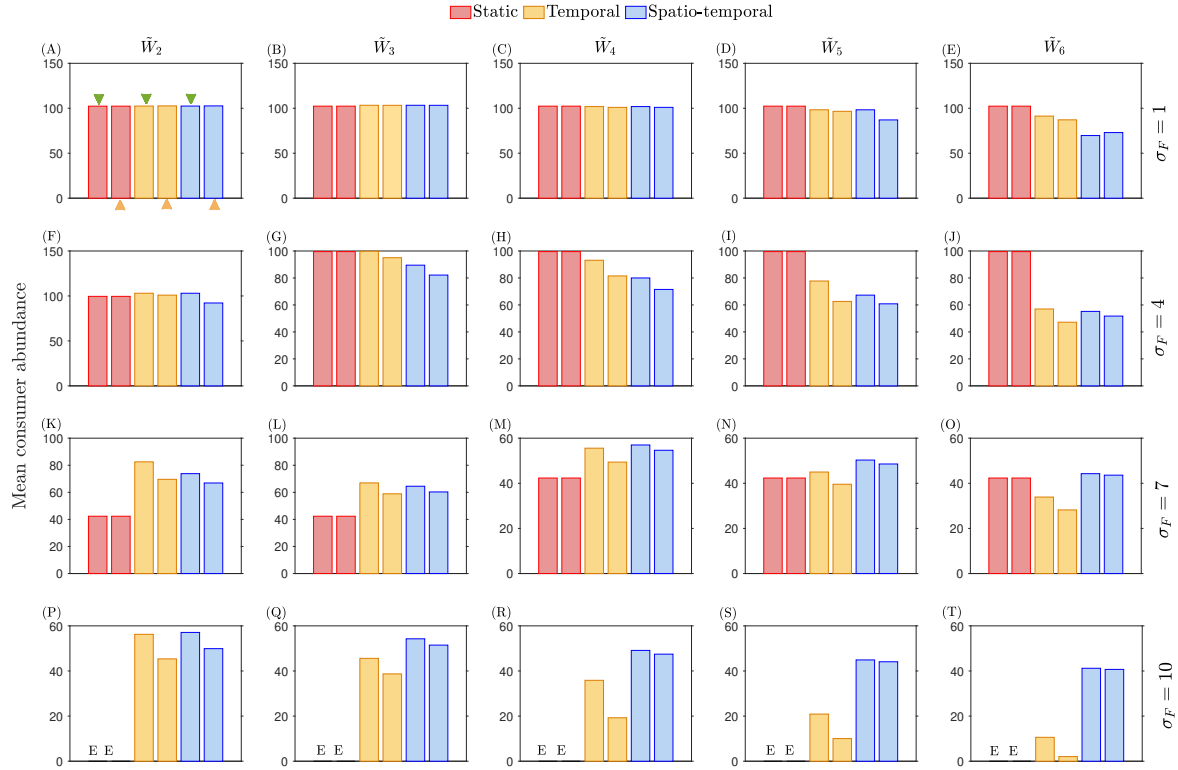


Figure 6. Robustness of consumer-resource dynamics along variations in the daily minima and maxima of the warming scenarios (warmer winters and hotter summers). In all the panels, $(\tilde{W}_2, \dots, \tilde{W}_6)$ correspond to the daily changes in the minimum and maximum temperatures. For instance $\tilde{W}_i$ corresponds to $\alpha = i$, $\beta = i + 1$ when experiencing warmer winters. $\tilde{W}_i$ corresponds to $\alpha = i + 1$, $\beta = i$ when experiencing hotter summers. The bars corresponding to the downward arrow give the mean abundance under warmer winters. The bars corresponding to the upward arrow represent the mean abundance under hotter summers. Cases marked with E depict the warming-driven extinction of the consumer.

When the daily change in the minimum and maximum (Min_T and Max_T , respectively)

313 temperature is low ($\tilde{W}_2, \tilde{W}_3, \tilde{W}_4$), the consumer abundance at low σ_F is same irrespective of
 314 the habitat as well as the climate warming scenario (Figs. 6(A)-6(C)). Therefore, suggesting
 315 no significant contribution of relocating to cooler habitats towards community abundance. Of
 316 note, at low amplitudes, access to the refugium depicts low consumer abundance with static
 317 habitat being most beneficial (Figs. 6(A)-6(J)). However, as the amplitude of fluctuation
 318 increases, the refugium appears to be most profitable in sustaining consumer abundance,
 319 followed by temporal and static conditions (Figs. 6(K)-6(T)). This result holds for changes
 320 in the daily minima and maxima ranging from the case $\tilde{W}_1$ to $\tilde{W}_6$. At $\sigma_F \approx 10^\circ\text{C}$, while
 321 consumers do not persist in the static conditions, temporal habitat leads to a decline in
 322 consumer abundance along changing values Min_T and Max_T . However, movement to refugia
 323 promotes species persistence and buffers the impact of warming. Therefore, our results hold
 324 good for varying ranges of Min_T and Max_T .

325 *Stability of the C-R dynamics under varying thermal regimes*

326 In addition, to comprehend species' persistence through changes in their abundance, it is
 327 fundamental to study system dynamics and its resilience. The resilience of a system is a
 328 measure of its stability, which asserts that a system, if stable, will always return to its initial
 329 stable condition on being perturbed by tiny external disturbances ([Recknagel 1985](#)). We
 330 now study the stability of the C-R dynamics in the presence of the thermal refugium, and
 331 varying warming scenarios. In the presence of the temperature-dependent parameters, the
 332 C-R interaction (Eqns. (1)) can be expressed as a piecewise affine “switching” system, as
 333 below:

$$\frac{d\mathbf{X}}{dt} = \mathbf{f}(\mathbf{X}, t) = \begin{cases} A_1\mathbf{X}(t), & \text{for } L_t = 1 \\ A_2\mathbf{X}(t), & \text{for } L_t = 0 \end{cases} \quad (6)$$

334 where $\mathbf{X} = [R \ C]'$ (with $'$ is the notation indicating the transpose operation) is a 2×1 vector
 335 in the state space, and the 2×2 matrices A_1 and A_2 define interaction sub-systems 1 and 2

336 (from Eqns. (1)-(5)), respectively, such that:

$$A_1 = \begin{bmatrix} r(T_R) (1 - Rq(T_R)) & -\frac{a_C(T_C)R}{R+R_h} \\ \frac{e_C a_C(T_C)C}{R+R_h} & -m_C(T_C) \end{bmatrix}, \quad (7a)$$

337 and

$$A_2 = \begin{bmatrix} r(T_R) (1 - Rq(T_R)) & 0 \\ 0 & -m_C(T_C) \end{bmatrix}. \quad (8a)$$

338 Particularly, A_1 corresponds to the consumer-resource dynamics when the consumer inhabits
 339 the feeding area. A_2 represents C - R dynamics when the consumer retreats to the refugium.
 340 Thus, the C - R interaction switches between the vector field characterised by A_1 and A_2
 341 depending upon the location and body temperature of the consumer.

342 Let us consider that a periodic orbit starts at time $t_o = \tau_o$, exhibits N number of switch-
 343 ings obtained at time $t_1 = \tau_1, t_2 = \tau_2, \dots, t_N = \tau_N$ to complete one cycle at $t_{N+1} = \tau$, such
 344 that $\mathbf{X}(\tau) = \mathbf{X}(\tau_o)$. We study period-to-period decrease or increase in the perturbation
 345 around the periodic orbit by calculating *fundamental solution matrix/Monodromy matrix*
 346 (Giaouris et al 2008, Klausmeier 2008):

$$\begin{aligned} \Phi(\tau_o + \tau, \tau_o, \mathbf{X}(\tau_o)) &= \Phi(\tau_o + \tau, \tau_{N+}, \mathbf{X}(\tau_{N+})) \mathbf{S} \Phi(\tau_{N-}, \tau_{N-1+}, \mathbf{X}(\tau_{N-1+})) \mathbf{S} \dots \\ &\dots \Phi(\tau_{2-}, \tau_{1+}, \mathbf{X}(\tau_{1+})) \mathbf{S} \Phi(\tau_{1-}, \tau_o, \mathbf{X}(\tau_o)). \end{aligned} \quad (9)$$

347 Here, τ_i- denotes the time instant just before switching, and τ_i+ is the time instant just
 348 after the switching. Since the system is non-autonomous, we obtain the fundamental matrix
 349 between any time interval (t_i, t_j) by solving the matrix differential equation:

$$\frac{d\Phi(t_j-, t_i+, \mathbf{X}(t_j))}{dt} = \mathbf{A}(\mathbf{t})\Phi(t_i, t_j, \mathbf{X}(t_j)), \quad (10)$$

with initial condition $\Phi(t_o, t_o, \mathbf{X}(t_o)) = \mathbf{I}$, and $\mathbf{A}$ (A_1 or A_2) is the subsystem defined within the time interval. $\mathbf{S}$ is the *saltation/jump* matrix evaluated at the switching instant τ_i , $i = 1, 2, \dots, N$. The eigenvalues of the fundamental solution matrix are termed as Floquet multipliers essentially determining the time evolution of the perturbation around periodic orbits (Klausmeier 2008). Importantly, to calculate Floquet multipliers it is important to consider the change in the vector field at a switching event. In context, *saltation/jump* matrices represent a jump in the system from one vector field to another. Let at the switching instant, the periodic orbit passes from a subsystem with a given vector field $\mathbf{f}_-(\mathbf{X}(t))$ to the subsystem having vector field $\mathbf{f}_+(\mathbf{X}(t))$, the saltation matrix is given by:

$$\mathbf{S} = \mathbf{I} + \frac{(\mathbf{f}_- - \mathbf{X}(t)) - (\mathbf{f}_+ - \mathbf{X}(t))\mathbf{n}'}{\mathbf{n}'\mathbf{f}_+}, \quad (11)$$

with $\mathbf{n}' = [1 \ 0]$ as the vector normal to the switching surface (with $'$ is the notation indicating the transpose operation). The vector field evaluated on one side of the switching manifold, i.e., $\lim_{t \uparrow \tau_i} \mathbf{f}_-(\mathbf{X}(t))$, is abbreviated as $\mathbf{f}_-$ and $\lim_{t \downarrow \tau_i} \mathbf{f}_+(\mathbf{X}(t))$, is abbreviated as $\mathbf{f}_+$. Thus, when the system switches from the feeding arena to the refugium arena, we have

$$\mathbf{S} = \mathbf{I}_{2 \times 2} + \begin{bmatrix} \frac{-a_C(T_C)C}{r(T_R)(R+R_h)(1-Rq(T_R))} & 0 \\ \frac{ea_C(T_C)C}{r(T_R)(R+R_h)(1-Rq(T_R))} & 0 \end{bmatrix}, \quad (12a)$$

and if the system switches its dynamics from the refugium to the feeding arena, we have

$$\mathbf{S} = \mathbf{I}_{2 \times 2} + \begin{bmatrix} \frac{a_C(T_C)C}{(R+R_h)(r(T_R)(1-Rq(T_R)) - \frac{a_C(T_C)C}{R+R_h})} & 0 \\ \frac{-ea_C(T_C)C}{(R+R_h)(r(T_R)(1-Rq(T_R)) - \frac{a_C(T_C)C}{R+R_h})} & 0 \end{bmatrix}. \quad (13a)$$

We find that the Floquet multipliers for each of the thermal regimes lie within the unit circle, thereby depicting the existence of stable oscillatory solutions of the C - R system. The access to the refugium in each thermally variable scenario depicts higher resilience of the system

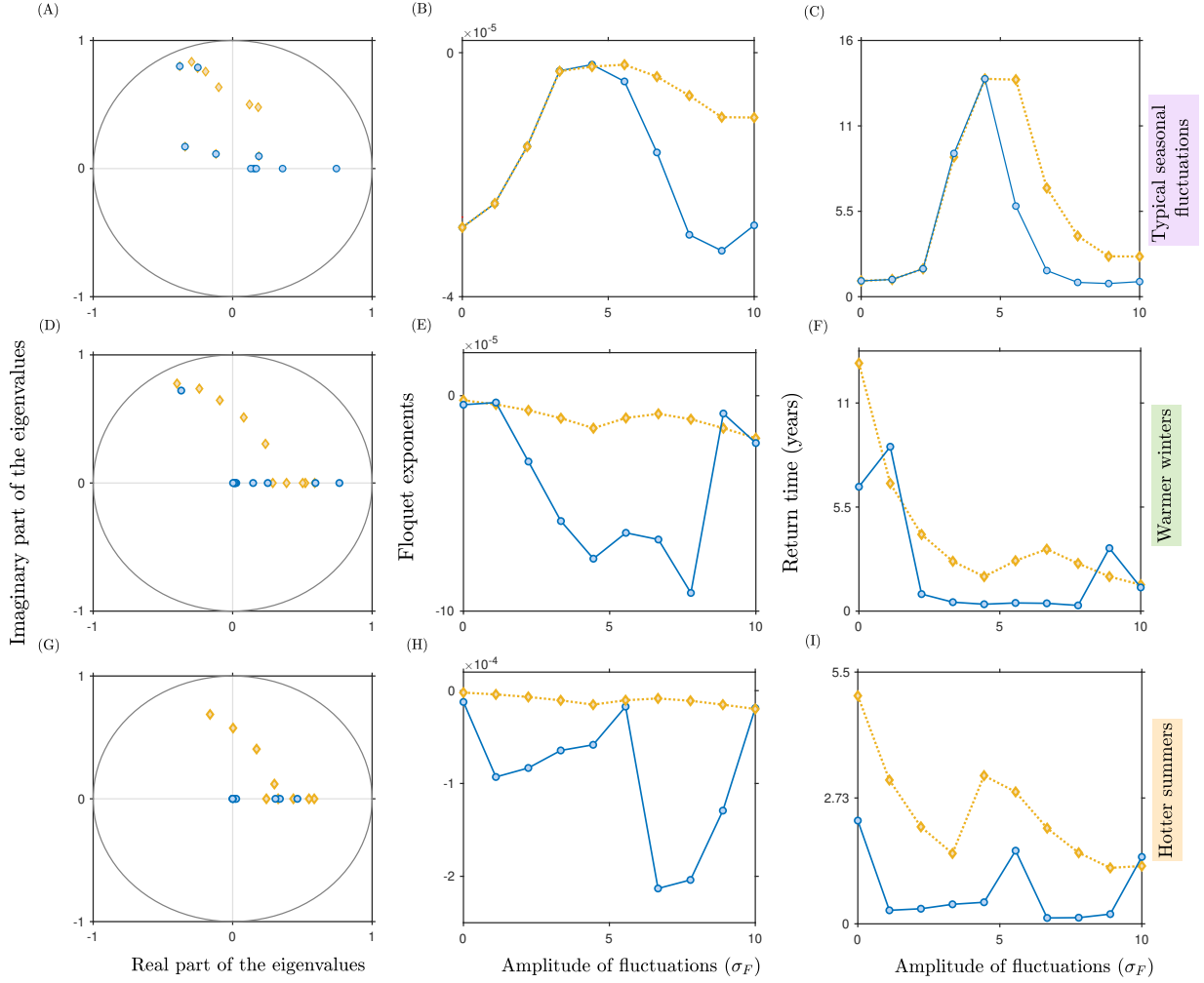


Figure 7. Stability analysis of the consumer-resource system for varying habitat as well as thermal variability conditions. (A), (D), (G) Loci for the Floquet multipliers for temporal and spatio-temporal cases. (B), (E), (H) Dominant eigenvalues of the Monodromy matrix representing Floquet exponents along the amplitude gradient, and (C), (F), (I) Return times of the consumer-resource system estimated as the reciprocal of the dominant eigenvalue of the Monodromy matrix. It demonstrates the time required for the system to reach $\approx 37\%$ of the initial perturbation displacement.

as compared to the temporal case (Fig. 7). In the typical seasonal fluctuations, the C - R periodic orbits are more stable (minimum return time) at low and high (extreme) values of σ_F (Figs. 7(A)-7(C)). Contrasting to it, the system equilibrates more quickly following a perturbation at the intermediate amplitude of thermal fluctuations for the other two warming scenarios (Figs. 7(E)- 7(F), and Figs. 7(H)-7(I)). The return time for the temporal habitat, in each of the warmer winters and hotter summers, is higher as compared to the spatio-temporal

habitat (Figs. 7(F)-7(I)). It, therefore, highlights that thermal refugia during hotter summers can be relatively more beneficial than during warmer winters and typical fluctuations, for ecological interactions both in terms of species persistence and functional stability.

Discussion

Identification and management of thermal refugia to support the persistence of species exposed to rapid climate warming has gained attention lately (Keppel et al 2012, Ashcroft 2010). Yet, the usefulness of thermal refugia under different warming scenarios is often overlooked. Here, we evaluate the reliability of refugia to enhance population persistence under changing warming conditions. We find that refugia are more effective in promoting species persistence and maintaining community functioning, specifically under high amplitude thermal fluctuations. Our result corroborates with a recent empirical investigation (Storlazzi et al 2020) examining the phenomenon of internal tides as thermal refugia for corals. The study incorporates diurnal temperature fluctuations, similar to the higher amplitudes observed in our own work, and identifies a delay in coral bleaching when thermal refugia are present. However, this contrasts with a previous study that suggests access to refugia enhances consumer abundance (Fey and Vasseur 2016), regardless of the amplitude of thermal fluctuations. Our finding is an aftermath of the unimodal thermal response curves of species foraging behaviour. Particularly, when temperature fluctuations reach high amplitudes, the attack rate of the consumer in its feeding habitats decreases significantly while metabolic demands increase exponentially. Consequently, consumers experience starvation in their feeding regions coupled with greater metabolic needs. However, refugia provide favourable conditions that mitigate the impacts of warming, allowing consumers to alleviate these challenges. Given that thermal refugia play a pivotal role in balancing the trade-off between maximizing resource acquisition and performance, it is imperative for consumers to relocate to refugia for an adequate duration in order to optimize this trade-off, especially in the presence of high amplitude temperature fluctuations.

The significance of refugia decreases at habitats with lower amplitude of thermal fluctu-

ations and high mean temperatures (see Fig. 3). At lower amplitudes the metabolic needs of the consumer in the feeding region are low, and it has an added energetic benefit due to the availability of the resource. On switching to the refugium with similar metabolic demands, its performance reduces due to no resource acquisition. Ebersole et al (2001) reports the potential impact of warm stream temperatures on the distribution and abundance of Pacific salmon, specifically rainbow trout. They emphasised that while the refugia offer some relief and allow rainbow trout to persist, their overall benefits may be reduced in streams experiencing high mean temperatures. In a similar line, we report that switching to refugia may not be advantageous for population abundance under projected climate change conditions, particularly at high mean temperatures and low amplitude fluctuations.

Furthermore, research suggests the prevalence of hotter weather conditions on the Earth’s surface with long summers (Pfleiderer et al 2019). We find that hotter summers are more detrimental to species persistence than the warmer winters and typical seasonal fluctuations. Therefore, while we uncover the effects of the amplitude of fluctuation on the usefulness of refugia, the role of different climate scenarios is equivalently important. We show that refugia are most advantageous in regions characterized by hotter summers, where they provide substantial benefits. In contrast, in regions with typical seasonal fluctuations and warmer winters, the cost associated with shifting to refugia may outweigh the thermal stress relief it offers. These outcomes result in a distinction in the utility of refugia based on the latitudinal variation of species. Specifically, temperate and Mediterranean species have evolved to thrive in areas with pronounced thermal fluctuations and low mean temperatures, whereas tropical species have adapted to function optimally under conditions of weak temperature fluctuations but with high mean values (Tewksbury et al 2008, Amarasekare and Johnson 2017). As a result, refugia may confer benefits to temperate and Mediterranean species, but they may not be effective for species evolving in tropical regions. This finding presses upon the necessity for additional strategies and measurements, beyond the preservation of refugia, to mitigate the impact of ongoing climatic conditions on the persistence of species.

We also perform our analyses for variations in the refugium quality (see Supplementary Information SI-1.4, Fig. SI-1.10), the time-scale of ecological dynamics (see Supplementary Information SI-1.5, Figs. SI-1.11–SI-1.13). Additionally, refugia can also be characterised by regions where species may relocate to increase their body temperatures during low mean temperatures, termed basking areas (see Supplementary Information SI-1.6, Fig. SI-1.14). Our results are consistent with selective adaptation to refugia in each of these cases, highlighting the role of variations in thermal conditions towards identification and management of such habitats.

Another applicability of refugia is their utility during extreme events, such as periods of heat waves, storms, etc (Kunze et al 2022). We find that during extreme weather conditions, the advantage of species colonisation or habitat selection into refugia is subject to species body size (Fig. 5). Particularly, for small-sized species, movement to refugia elevates consumer abundance at low amplitudes, which is not observed for larger organisms. At high amplitude of fluctuations, however, species undergo extirpation irrespective of the movement to refugia as well as their body size. Thereby, challenging the usefulness of identifying and adapting to thermally retreating habitats. If estimating the future loss of refugia and developing management strategies to preserve it is an important practice (Dixon et al 2022, Kurylyk et al 2015), it is equally vital to find when and where refugia appear beneficial for populations from a biodiversity conservation perspective. In all, we find that relocation to refugia might not always be a key strategy to adapt to climate change, but selective adaptation to habitats with thermal heterogeneity can overcome the impacts of warming. Consequently, when devising management strategies in regulating climatic conditions, trends in the mean and amplitudes of thermal fluctuations demand consideration, rather than the magnitude alone.

Further, stability analysis of the system through the derivation of Floquet multipliers (see Fig. 7) shows that the existence of refugia increases the resilience of species towards warming. It is yet to be shown that refugia access is the optimal adaptation strategy for

preserving biodiversity in general. Our study is among the first few to discuss consumer-resource dynamics and the impacts of refugia access across disparate climate regimes. Our results have implications on discerning environmental conditions and warming regimes which require refugia access. It is left for policymakers to culminate from theoretical findings and real observations whether to identify refugia in a highly fluctuating environment or switch to alternative cost-effective strategies, if any, for safeguarding vulnerable species. Refugia lacking resources are practical when consumers lodge for short spans in the refugia and switch to feeding arena in regular intervals (Rohr and Palmer 2013, Bevelhimer and Adams 1993). Whilst this is true, identifying natural refugia enabled with resources might aid in expanding its utility to even larger body-sized organisms in periods of extreme events. We present here a premier study investigating the significance of refugia on the persistence of a resource-consumer system, while species dwell in a community interacting with other individuals of the same or different taxa. A study on the effectiveness of refugia in a network of resource-consumer competing for food and space is a promising future direction.

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